

OAHU'S MARINE PROTECTED AREAS HAVE LIMITED SUCCESS IN PROTECTING  
CORAL REEF HERBIVORE FUNCTIONAL ASSEMBLAGES

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## **Abstract**

Herbivorous fishes and urchins improve reef resilience by removing algae that might otherwise smother corals, yet herbivores are frequently targeted by fishers. The deleterious effects of fishing on herbivore populations can be limited through the establishment of no-take marine protected areas (MPAs). In Hawai‘i, the state government is planning to effectively manage 30% of its nearshore waters by 2030, which may include the expansion of an existing MPA network. During 2018-19, I conducted visual diver surveys to compare the biomass, density, and size structure of reef fish and urchin populations inside and outside of four of O‘ahu’s current MPAs to determine if they are effectively protecting herbivore functional assemblages. Using photo-quadrats, I also characterized the benthos, including post-dive, microscopic identification of common taxa in algal turfs that were collected, to evaluate possible secondary effects of differential herbivory on benthic algal communities at multiple sites within each region. While protected areas had a higher total biomass of herbivore populations, the magnitude of the effect varied depending on region (e.g. Hanauma Bay, Kāne‘ohe, Pūpūkea, and Waikīkī) and functional guild (e.g. grazer, scraper, browser, and urchin). While the biomass of individual functional guilds often differed between protected and unprotected sites, Hanauma Bay was the only MPA with a significant difference in the herbivore assemblage between protected and unprotected sites. Herbivore populations were also associated with benthic assemblages, and differences in the turf community were correlated with differences in the herbivore community, consistent with previous findings that herbivore and benthic assemblages reciprocally structure each other’s communities. Urchins and grazing fishes accounted for the majority of herbivore biomass across regions, and the dominance of urchins suggests that they should be included in future evaluations of herbivory. Additionally, functional diversity and redundancy was low

across site and region, suggesting ecological processes are dominated by a single or few species. The small size structure of herbivorous fishes in MPAs across all regions also likely limits their population-level functional impact and fecundity. These results suggest that while the MPAs of O‘ahu benefit herbivore assemblages, their positive effect is limited and likely confounded by differences in habitat between protected and unprotected sites.

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## **Introduction**

Coral reefs are among the most diverse ecosystems in the world, and provide livelihoods for millions of people (Moberg and Folke 1999; Newton et al. 2007; Cinner et al. 2009; Darling and D'agata 2017). A recent assessment indicates that coral reefs in the main Hawaiian Islands may be worth up to \$33.57 billion/year (Bishop et al. 2011). However, reefs are increasingly threatened by anthropogenic stressors, such as overfishing, land-based sources of pollution (LBSP), and climate change (Pauly et al. 2005; Newton et al. 2007; Carpenter et al. 2008; Mora et al. 2018). The State of Hawai'i recently launched the "30 by 30" initiative with the goal of effectively managing 30% of its nearshore waters by 2030 with the intention of mitigating the effects of these stressors and maintaining the productivity and value of the reefs (DAR 2016). With these goals in mind, it is important to re-examine Hawai'i's protected areas, and assess their success in promoting reef health and resilience.

A recent survey by Chung et al. (2018) found the three most effective management interventions for promoting reef resilience in Hawai'i are establishing a network of herbivore fisheries management areas, banning parrotfish fishing, and establishing no-take MPAs – all actions that would bolster herbivore populations through some measure of protection. Herbivory is frequently cited as among the most important factors contributing to coral reef resilience by preventing algal dominance and overgrowth (Carpenter 1986; Tanner 1995; Bruggemann et al. 1996; Mumby et al. 2006b; Hughes et al. 2007; Bonaldo and Bellwood 2008; Rasher and Hay 2010; Hixon 2015; Chung et al. 2018). Herbivores consume algae that would otherwise compete with corals for space and limit coral settlement and recruitment, thus maintaining coral dominance (Carpenter 1986; Hughes et al. 2007). The role of herbivory in promoting reef



resilience is likely to become more important, as reefs are predicted to become more susceptible to incursion from at least one invasive alga under future warming scenarios (Veazey et al. 2019).

Coral recovery is further promoted by herbivore populations with complementary feeding modes that can target and remove different groups of algae (Burkepile and Hay 2008). The loss of functional herbivore guilds can trigger a regime shift (Folke et al. 2004). For example, the loss of grazing by the urchin *Diadema antillarum* triggered a coral-algal phase-shift on Caribbean reefs (Carpenter 1986; Mumby et al. 2006b, 2007), although this was predicated by substantial reduction in fish grazing arising from overfishing of herbivorous fishes (Bellwood et al. 2004; Nystrom et al. 2008) and nutrient enrichment from sub-marine groundwater discharge bringing in land-based sources of pollution (D'Elia et al. 1981). The risk of phase shifts can be mitigated if multiple species fulfill the same functional role and can compensate for the loss or reduction of another species (Bellwood et al. 2004; Nystrom et al. 2008). Therefore, reef resilience is dependent in part on herbivore populations with both high functional diversity and redundancy (Bellwood et al. 2003; Folke et al. 2004; Burkepile and Hay 2008; Hoey and Bellwood 2009; Johansson et al. 2013; Kelly et al. 2016).

Coral reefs were originally thought to promote high functional redundancy of herbivorous fishes (Odum and Odum 1955), which was supported by in situ observations suggesting that the vast majority of herbivores feed on turf algae (Hay and Taylor 1985; Kelly et al. 2016). However, there has been a recent movement for more detailed assessments of these functional roles (e.g. Brandl and Bellwood 2014; Adam et al. 2015). The functional role and ecological effect (e.g. grazing rate, bioerosion rate) of a fish can broadly be determined by combinations of unique traits (Mouillot et al. 2014), such as general diet (Edwards et al. 2014), body size (Bellwood and Choat 1990; Ong and Holland 2010), mobility (Norman and Jones

1984; Meyer and Schultz 1985; Nagelkerken et al. 2000), the period of the day in which they are active (Bellwood et al. 2006), their position in the water column (Gido 2003), and their schooling behavior (Meyer and Schultz 1985; Michael et al. 2013; Basford et al. 2016). Mouillot et al. (2014) termed these combinations “functional entities,” and found that while diverse fish assemblages may have more unique functional entities, a disproportionate number of species are packed into relatively few functional entities. Furthermore, 38% of the functional entities in the most speciose region had no functional redundancy (i.e. there was only one species of fish in that functional entity). Additionally, while Mouillot et al. (2014) treated herbivores as a single group, gut content analysis of herbivorous coral reef fishes suggests that there is complementarity between species in the taxa of algae consumed (Kelly et al. 2016). Thus, there is likely even less functional redundancy than previous observations and analyses suggest, and overfishing can result in removing a species with no functional equivalent (Brandl and Bellwood 2016; D’agata et al. 2016; Thiault et al. 2017). Given that the species composition of turf is influenced by both bottom-up factors such as nutrient enrichment and top-down factors such as grazing (Smith et al. 2001, 2010a; Stuercke and McDermid 2004), and that there is complementarity in the taxa of turf that herbivores consume (Kelly et al. 2016), it is likely that changes in herbivore assemblages drive changes in turf communities and vice versa, and altering either species assemblage can have cascading effects.

Despite recent developments in determining the exact functional roles of coral reef fishes, there is still benefit in using broader functional classifications as a framework for describing herbivore interactions with the benthos (Edwards et al. 2014). Herbivorous fishes are commonly split into three primary functional guilds based on their method of feeding: scrapers/excavators, grazers/detritivores, and browsers (Carpenter 1986; Green and Bellwood 2009). Scrapers (e.g.

*Scarus rubroviolaceus*) produce bite scars that promote crustose coralline algae (CCA) and coral recruitment (Bellwood 1995; Ong and Holland 2010; Smith et al. 2010), but large parrotfish bites can gouge/excavate substrate and lead to bioerosion (Bellwood and Choat 1990; Green and Bellwood 2009). Smaller grazers/detritivores (e.g. *Zebrasoma flavescens*) remove only individual filaments and partially graze on turfs, cropping the turf but allowing for rapid regrowth that can hinder CCA recruitment (Carpenter 1986). Additionally, while detritivores (e.g. *Ctenochaetus strigosus*) were previously treated as a separate functional guild, they have been shown to consume a substantial amount of algal turf along with detritus and are often grouped together with grazers in broader functional analyses (Green and Bellwood 2009; Marshall and Mumby 2012). Browsers (e.g. *Naso unicornis*) selectively feed on fronds of macroalgae (Green and Bellwood 2009; Kelly et al. 2016).

Jouffray et al. (2015) found that the functional makeup of herbivorous fish populations was among the most important factors dictating reef state across the Hawaiian archipelago, and that there are three primary regimes that exist throughout both the main Hawaiian Islands (MHI) and the northwestern Hawaiian Islands (NWHI): a calcifying regime with coral and CCA cover, a low complexity regime dominated by macroalgae and/or sand, and a turf regime. While all three herbivore functional guilds had a negative relationship with the macroalgae/sand regime, different functional compositions of reef fish were associated with the calcifying regime and the turf regime. In particular, grazer biomass had a positive relationship with the turf regime, whereas scraper biomass had a positive relationship with the calcifying regime. Therefore, while herbivores are important in managing macroalgal dominance, the functional makeup of those herbivores can lead to either calcifying or turf regimes.

While the functional composition of herbivorous fishes is important to the condition of a reef (Jouffray et al. 2015), healthy herbivore populations – and by extension, reef resilience – are threatened by unsustainable fishing practices (Newton et al. 2007; Williams et al. 2008; Houk et al. 2018a). Coral reef fisheries are historically difficult to manage being characterized by a wide diversity of captured species, fishing activities, and gear types (Graham et al. 2017), but reliable catch data are rare and life history information necessary for effective management is known for only about 1,200 out of 7,000 commonly exploited species (Froese and Pauly 2017). Roughly 55% of coral reef fisheries in the tropical Pacific are now overfished (Newton et al. 2007). Parrotfishes in particular are heavily targeted in coral reef fisheries (Williams et al. 2008; Houk et al. 2018b) and are highly sensitive to fishing pressure (Houk et al. 2018b). Given that larger parrotfish have higher grazing rates and bioerosion rates (Bellwood and Choat 1990; Bellwood 1995; Ong and Holland 2010; Smith et al. 2010), altering the size structure of parrotfish populations through fishing can affect their relative impact on the surrounding environment. Conversely, surgeonfishes are relatively resilient to fishing pressure (Houk et al. 2018b). Because grazers like surgeonfishes promote turf dominated environments (Jouffray et al. 2015), fishing potentially reduces the functional impact of parrotfishes by selecting for smaller grazing fishes (Houk et al. 2018b) which would promote turf or macroalgae regimes (Jouffray et al. 2015).

Unsustainable fishing practices are already threatening Hawaiian reefs (Williams et al. 2008; Gorospe et al. 2018). Of roughly two million reported commercial and non-commercial fishing trips a year in MHI, 1.7 million are reef fishing trips, and about half of those occur on O‘ahu alone (McCoy et al. 2018). O‘ahu’s herbivorous fish populations are severely depleted, with < 4% of parrotfish biomass than remote areas (Williams et al. 2008). Additionally, fishers

tend to target larger fishes, which are exponentially more fecund and produce larvae with greater survivorship than smaller fish (Birkeland and Dayton 2005). Williams et al. (2008) termed these large individuals in target species of fish “prime spawners,” and found that O‘ahu had < 3% prime spawner biomass than what was found in remote areas, and that only three mid-sized surgeonfish species contributed to O‘ahu’s total prime spawner biomass. However, fish biomass can increase up to 280% if human impacts are minimized (Gorospe et al. 2018), emphasizing the importance of protection and effective management.

Here, I assessed the effectiveness of O‘ahu’s protected areas in protecting herbivore assemblages. While previous studies suggested that the protected areas have greater herbivore biomass than the surrounding fished areas (e.g. Friedlander et al. 2007), few have assessed the role of protection on herbivore functional guilds and their size structure (Nash et al. 2016). Additionally, while urchins have a well-documented role in promoting reef resilience in the Caribbean (Carpenter 1986; Klumpp and Pulfrich 1989; Russ 2003), almost no studies have included urchins in their analyses of herbivore assemblages in Hawai‘i. Urchins can fulfill similar ecological roles as many herbivorous fish, such as by scraping algal turfs and consuming macroalgal growth (e.g. Mumby et al. 2007; Stimson et al. 2007; Sangil and Guzman 2016), and the mechanisms by which they feed can contribute to bioerosion (Carriero-Silva and McClanahan 2001; Griffin et al. 2003; Sangil and Guzman 2016). As such, I assessed herbivore community response by comparing the biomass, density, and size structure of grazers, scrapers, browsers, and urchins inside and outside four marine protected areas of O‘ahu. Additionally, I assessed indirect effects of protection on benthic communities, including taxonomic differences in the algal turf community, and tested the association between habitat factors and herbivore assemblages. Turfs were included in analyses because they are historically understudied in larger

ecological surveys and are often miscategorized as the term turf is inconsistently used (Connell et al. 2014), yet turf are a key component in the diet of most herbivorous fish (Hay and Taylor 1985; Kelly et al. 2016) and may be as competitive with coral as larger macroalgae (Birrell et al. 2008; Vermeij et al. 2008; Smith et al. 2010). Thus, the study sought to determine whether the current protected areas are in fact effectively managing O‘ahu’s herbivore resources, thereby providing a scientific foundation for the evaluation of these management areas.

## Methods

### *Study site*

Surveys were conducted from late June 2018 to June 2019 across four regions around O‘ahu (Figure 1): the north shore (Figure 2a, Pūpūkea Marine Life Conservation District, hereafter MLCD), Kāne‘ohe Bay on the windward east shore (Figure 2b, Moku o Lo‘e Marine Laboratory Refuge), Hanauma Bay in the southeast (Figure 2c, Hanauma Bay MLCD), and Waikīkī on the south shore (Figure 2d, Waikīkī MLCD). Surveys of each region were started and completed within a month with the exception of surveys along the north shore, which were split between November 2018 and June 2019 because of poor field conditions during persistent large winter swells.

Surveys were conducted with a stratified random sampling schema across two levels of strata: management (protected or unprotected) and habitat (i.e., colonized or uncolonized hardbottom). Habitat strata were included to account for variation in fish assemblages associated with habitat features (e.g. Friedlander et al. 2007b). Surveys in unprotected areas were delineated by a 1.5 km buffer extending beyond the bounds of the protected areas, although this buffer was extended to 2 km for Hanauma Bay because there was no suitable habitat within the original 1.5 km buffer and the need to maintain depth parity with surveys conducted within the MLCD. Colonized and uncolonized hardbottom were determined using a benthic map data in a GIS, where colonized hardbottom was designated as >10% coral cover (Coyne et al. 2003; Friedlander et al. 2006). Ten surveys were randomly located within each management x habitat stratum for a total of  $n = 40$  surveys in each region, following methods for sample optimization using these maps outlined by Friedlander et al. (2006). There were no colonized hardbottom polygons from the NOAA benthic habitat map within the Waikīkī MLCD. Surveys that were not at least 25 m

away from another survey location were discarded and replaced with another randomly selected survey coordinate to avoid pseudo-replication in fish surveys. Surveys were not conducted within the Waikīkī Fisheries Management Area (FMA) along the south shore of O‘ahu because of potential confounding effects of fishing because this FMA allows fishing in even numbered years while all the other MPAs in the study had permanent management restrictions on fishing.

### *Survey methods*

Reef fish visual diver surveys were conducted at each assessment site on 5 x 25 m transects at  $\leq$  12 m depth. All fish (not just herbivores) were sized (cm total length) and identified to species by a diver swimming at constant speed (~15 min each transect). Urchins were also counted and identified to species within a 2 x 25 m transect using the same center line as the fish surveys. The first 25 urchins of each species were sized by measuring test diameter (to nearest cm) to provide an estimate of overall size structure. While previous studies assessing urchin herbivory have focused exclusively on diadematids (e.g. Tootell and Steele 2016), echinometrid urchins have been found to be sources of both grazing and bioerosion (Sangil and Guzman 2016), and so were included in these surveys. Herbivores were later stratified into general feeding guild (scraper/excavator, browser, grazer, and urchin) based on descriptions in the literature (Table 1; Green and Bellwood 2009; Randall 2010; Froese and Pauly 2017). Detritivores, such as *Ctenochaetus strigosus*, were grouped together with grazers as previous studies indicate that they consume a substantial amount of turf (Marshall and Mumby 2012). Finally, scrapers and excavators were grouped together, as only two *Chlorurus* spp. exceeded the 35 cm threshold associated with excavating substrate while feeding (Green and Bellwood 2009). Fish length was converted to biomass using  $W = aL^b$ , where  $W$  is fish biomass (g),  $L$  is total fish length (TL in



cm), and  $a$  and  $b$  are species-specific allometric scaling constants from publicly available sources (e.g. Kulbicki et al. 2005; Froese and Pauly 2017). Total length (TL) was converted to standard length (SL) or fork length (FL) as necessary based on available linear scaling data (e.g. Froese and Pauly 2017). Hawai‘i specific constants were used when possible. Urchin test diameter was converted biomass using the same formula, where  $L$  is test diameter and  $a$  and  $b$  are allometric scaling constants from previously published data (McClanahan 1988; Regalado et al. 2011). The biomass conversion for *Diadema sauvisignii* was generalized across all diadematids and *Heterocentrotus mamillatus*, and the biomass conversion for *Echinometra mathaei* was generalized across all remaining echinometrids and *Eucidaris metularia* due to a lack of species-specific scaling constants.

Benthic measurements were taken concurrent with the fish and urchin surveys. Benthic photo quadrats were taken every other meter using a monopod 0.6 m off the substrate. Images were analyzed using CoralNet (Beijbom et al. 2012, 2015) by identifying the substrate under each of 100 randomly points per image down to the lowest taxonomic level for a total of 1,300 points per transect. The optimum number of points per image was determined by a power analysis conducted by Brown et al. (2004). Species identifications were later grouped into broader functional categorizations (coral, CCA, turf, sediment-laden turf, sponge, green macroalgae, red macroalgae, brown macroalgae, large filamentous cyanobacteria, and other mobile/sessile invertebrate) to simplify analysis and data visualization. However, non-aggregated data were tested prior to grouping the benthic data, and it was determined that simplifying the data did not obscure overall trends in the data.

Additionally, rugosity was measured by carefully laying a 1.3 cm link chain across the first 10 m of the centerline of each transect (Risk 1972; McCormick 1994). A rugosity index was

calculated by taking the ratio of horizontal reef distance to the distance along the reef surface contour (i.e. the length of the chain laid out), with an index value of 1 indicating no reef complexity. Finally, two 1 cm<sup>2</sup> turf samples were collected as close to the centerline as possible from each transect with forceps for a total of  $n = 80$  samples in each region. Turf samples were collected from opposite ends of each transect to account for as much within-transect spatial variability in the turf assemblage as possible. Samples were preserved in 3–4% formalin for at least 48 hrs until further analysis.

Turf samples were prepared for analysis by first isolating filaments from as much of the sediment/detritus as possible. Turfs were then placed on a slide and decalcified with 1–5% HCl solution and stained with 1% Aniline blue in filtered sea water. Slides were then preserved with a distilled water solution of 25% Karo 2% Phenol solution under a cover slip following Tsuda and Abbott (1985). Turfs were then identified to the lowest taxonomic level under microscope in the lab with the assistance and use of available identification keys (Price and Scott 1992; Abbott 1999; Abbott and Huisman 2004; Guiry and Guiry 2019). Algal processing time (45 min–3 hrs per sample) was not sustainable, thus turf analysis was reduced to one sample from each transect following the complete analysis of samples from Kāneʻohe Bay and the Waikīkī protected site.

### *Data analysis*

Total biomass (g m<sup>-2</sup>), herbivore biomass, and the biomass of each herbivore functional guild in protected and unprotected sites across Oʻahu and in each region was  $\log(\text{biomass} + 1)$  transformed as raw data were positively skewed and non-normal. Data were compared between protected and unprotected sites in each guild and region using generalized linear models (GLMs). The  $\log(\text{biomass} + 1)$  transformed data were then used to characterize herbivore

functional assemblages (scraper/excavator, browser, grazer, and urchin biomass) among regions and protection status using non-metric multidimensional scaling (nMDS) with environmental vectors drawn representing rugosity and depth using the vegan package in R (Oksanen 2011; R Development Core Team 2011). Territorial damselfish were excluded from analyses because they are not targeted in fisheries (Edwards et al. 2014) and were absent from the majority of transects. Piscivore biomass between protected and unprotected sites was also compared using GLMs to test for any possible effects on herbivore biomass due to predation. Herbivore communities from protected sites were then compared with communities from outside the protected sites using PERMANOVA in each region, with rugosity and depth as additional factors. Pairwise-permutation tests were used to determine which communities were distinct from each other in the case of a significant result. PERMANOVA was used to assess the multivariate community response in addition to repeated GLMs for each functional guild to assess whole community response to protection in addition to individual guild response. Size structure of the fish functional guild were compared between protected and unprotected sites using Kolmogorov-Smirnov tests (e.g. Clements and Hay 2018) and were visualized using probability density histograms.

Species richness, inverse-Simpson's diversity, evenness, and reserve capacity were used as metrics of within-guild species and functional diversity and redundancy (Magurran 1988). Reserve capacity represents the collective ability for all other species to fulfill a similar ecological function as the dominant species in a functional guild and is defined as follows:

$$RC = \frac{\sum_{i=1}^n (A_i - D_i)}{\sum_{i=1}^n A_i}$$

Where  $RC$  is the reserve capacity,  $A$  is the total fish abundance in a functional guild on transect  $i$ , and  $D$  is the abundance of the numerically dominant species in a functional guild on transect  $i$  (Johansson et al. 2013). Reserve capacity, species richness, inverse-Simpson's diversity and evenness were compared among regions and protection status using GLM Two-Way ANOVAs. Reserve capacity was plotted against diversity and evenness was plotted against species richness for visualizing relationships between diversity measures. Test statistics and summary statistics are available in the supplementary materials (Appendix 1, Appendix 2).

Associations between herbivore functional assemblages and benthic community data across O'ahu and at individual regions were assessed using canonical analysis of principal components (CAP) in R (Oksanen 2011; R Development Core Team 2011). CAP was used to allow for correlation between predictors (i.e. protection status and the different benthic categories). Benthic data were arcsine square root transformed prior to analysis. The significance of the benthic predictors was assessed using a permutation test for CAP in R (Oksanen 2011; R Development Core Team 2011).

Differences in turf communities across regions and sites were visualized using nMDS and tested using PERMANOVA. Pairwise-permutation tests determined which communities were distinct from each other in the case of a significant result. A complete list of turf species is in the supplementary materials (Appendix 3).

## Results

11,911 fish in 114 species and 14,643 urchins were observed throughout the surveys. 16 species of grazer were observed from six genera, four species of scraper were observed from two genera, five species of browser were observed from three genera, and 10 species of urchin were observed from seven genera. Herbivores accounted for the majority of the biomass of reef fishes and urchins inside and outside the protected sites across all regions (Table 2). Kāneʻohe sites had lower total herbivore biomass than all other regions, driven by low urchin density and biomass; herbivores accounted for 61% and 67% of the total biomass at the protected and unprotected sites in this region, respectively (Table 2). Herbivores accounted for 83 – 98% of the biomass at all other sites. Urchins accounted for the greatest biomass of all herbivores in all sites (51 – 93% of herbivore biomass) except for the Kāneʻohe Bay and Waikīkī protected sites, where they accounted for 5% and 33% of total herbivore biomass, respectively. Grazers were the most abundant herbivores at these sites, accounting for 74% of herbivore biomass in the Kāneʻohe Bay protected site and 48% in the Waikīkī protected site. Grazers accounted for 19 – 32% of total herbivore biomass in all other sites. While there was no significant difference in total (fish and urchin) biomass inside and outside the protected sites when regions were pooled (GLM,  $\chi^2 = 1.08$ ,  $P = 0.29$ ), there was significantly greater herbivore biomass inside protected sites (GLM,  $\chi^2 = 1.08$ ,  $P = 0.29$ ), driven by higher grazer ( $\chi^2 = 37.3$ ,  $P = 1.0e-09$ ), scraper ( $\chi^2 = 10.2$ ,  $P = 0.001$ ), and browser ( $\chi^2 = 20.9$ ,  $P = 4.7e-06$ ) biomass inside the protected sites (Figure 3a). This trend was largely influenced by Hanauma Bay, which had higher total biomass inside the protected site (Figure 3d, GLM,  $\chi^2 = 5.1$ ,  $P = 0.02$ ), as well as higher herbivore biomass ( $\chi^2 = 28.1$ ,  $P = 1.1e-07$ ) driven by higher grazer biomass ( $\chi^2 = 63.4$ ,  $P = 1.66e-15$ ), scraper biomass ( $\chi^2 = 22.8$ ,  $P = 1.8e-06$ ), and browser biomass ( $\chi^2 = 43.9$ ,  $P = 3.43$ ). Additionally, while grazer, scraper, and

browser biomass was 1.8–2.2 times greater inside protected sites when all regions were pooled, biomass for these functional guilds was 5–17 times greater inside the protected site in Hanauma Bay (Table 3). These trends were less pronounced at other regions; only grazer (Figure 3b, GLM,  $\chi^2 = 4.41$ ,  $P = 0.04$ ) and urchin biomass ( $\chi^2 = 5.19$ ,  $P = 0.02$ ) were greater inside the north shore protected area than outside, but there was no significant difference in total biomass ( $\chi^2 = 2.11$ ,  $P = 0.15$ ) or in any of the other herbivore functional guilds. Kāneʻohe Bay had greater grazer biomass inside the protected area (Figure 3c, GLM,  $\chi^2 = 8.82$ ,  $P = 0.03$ ), but there was no significant difference in total biomass ( $\chi^2 = 0.002$ ,  $P = 0.96$ ) or in the biomass of any of the other herbivore functional guilds. Total biomass was 1.1 times higher in the unprotected site at Waikīkī (Table 3), but this difference was not significant (Figure 3e,  $\chi^2 = 0.005$ ,  $P = 0.95$ ). Browser biomass was 14.4 times greater inside the Waikīkī protected site ( $\chi^2 = 14.4$ ,  $P = 1.3e-04$ ), but there was no significant difference in biomass for any other functional guild. Piscivores accounted for the greatest proportion of total biomass in the Kāneʻohe Bay unprotected site, where they made up 10% of the total biomass. However, they only accounted for only 0.9% – 7% of the total biomass at all other sites. Hanauma Bay was the only region in which there was a significant difference in piscivore biomass between protected and unprotected sites (GLM,  $\chi^2 = 13.7$ ,  $P = 2.0e-04$ ), where biomass was 5.3 times greater inside the protected area than outside (Table 3).

Ordination of the herbivore communities suggested that Kāneʻohe Bay had unique herbivore assemblages, likely driven by low browser and urchin biomass, with scrapers proportionally accounting for most of the biomass (Figure 4). This pattern was confirmed by results from a PERMANOVA test, which showed differences in regions accounted for much of the variation in the herbivore functional assemblages (Pseudo- $F = 24.8$ ,  $R^2 = 0.30$ ,  $P = 0.001$ ).

Additionally, the communities in the unprotected site outside of Hanauma Bay were distinct from other herbivore communities, likely driven by low biomass across all functional guilds. Surveys with higher urchin biomass seemed to be distinct from those with more herbivorous fish, and oriented away from other surveys in the ordination space. There was substantial overlap between herbivore communities in protected sites at Hanauma Bay, the north shore, and Waikīkī, and pairwise-permutation tests suggested there was no significant difference between herbivore functional assemblages in these regions (Hanauma protected vs. Waikīkī protected: Pseudo-F = 2.80,  $R^2 = 0.09$ , P-adj = 1.00; Waikīkī protected vs. north shore protected: Pseudo-F = 2.07,  $R^2 = 0.07$ , P-adj = 1.00, Hanauma protected vs. north shore protected: Pseudo-F = 4.72,  $R^2 = 0.11$ , P-adj = 0.08). Protected sites had different herbivore functional assemblages from unprotected sites (PERMANOVA, Pseudo- F = 17.86,  $R^2 = 0.07$ ,  $P = 0.001$ ), although this pattern was solely driven by Hanauma Bay, the only region with a significant difference in herbivore functional assemblages between protected and unprotected sites (pairwise permutation test, Pseudo-F = 21.9,  $R^2 = 0.39$ , P-adj = 0.03). There was a significant interaction effect between region and protection (PERMANOVA, Pseudo- F = 2.22,  $R^2 = 0.03$ ,  $P = 0.02$ ), driven by unique communities in Kāneʻohe Bay and in the unprotected site outside Hanauma Bay. Rugosity (PERMANOVA, Pseudo- F = 4.99,  $R^2 = 0.02$ ,  $P = 0.007$ ) and depth (PERMANOVA, Pseudo-F = 5.33,  $R^2 = 0.02$ ,  $P = 0.003$ ) were both significant predictors of herbivore assemblages.

Constrained axes from a canonical analysis of principal coordinates with protection and benthic communities as predictors for herbivore assemblages explained 11.7% of the variation in the herbivore functional assemblages around Oʻahu (Figure 5). The first constrained axis explained 7.6% of the constrained variation, and the second constrained axis explained 2.3% further. Coral cover was aligned strongly with the second constrained axis towards herbivore

communities at protected sites. Urchins appeared to be more associated with turf, sediment-laden turf, red macroalgae, and sand. The constrained axes were significant predictors of herbivore functional assemblages (Permutation test,  $\text{Pseudo-F}(9, 140) = 2.07$ ,  $P = 0.001$ ). These trends held true at the regional scale, and the north shore was the only region where the total variation explained by the constrained axes was not significant (Figure 6a, Permutation test for capscale,  $\text{SSQ}(9.2, 36.2)$ ,  $\text{pseudo-F}(8,31) = 0.99$ ,  $P = 0.49$ ). Coral cover was strongly associated with herbivore communities in Hanauma Bay (Figure 6c).

There was a significant difference in grazer and scraper size distributions between protected and unprotected sites when all regions were combined (Grazers: Kolmogorov-Smirnov test,  $D = 0.06$ ,  $p = 0.002$ ; Scrapers:  $D = 0.09$ ,  $P = 0.008$ ), with some evidence of size truncation at unprotected sites (Figure 7). However, these trends were not uniform across all regions. There was no significant difference in grazer size distributions at the north shore (Figure 8a; Kolmogorov-Smirnov test,  $D = 0.07$ ,  $P = 0.06$ ), with no apparent size truncation in unprotected sites. Additionally, while there was no significant difference in browser size distribution when all regions were combined (Figure 7b, Kolmogorov-Smirnov test,  $D = 0.09$ ,  $P = 0.32$ ), there was a significant difference in browser size distributions at each individual region (Figure 9a, North Shore:  $D = 0.53$ ,  $P = 2.8\text{e-}14$ ; Figure 9b, Hanauma:  $D = 0.59$ ,  $P = 2.9\text{e-}06$ ; Figure 9c, Waikīkī:  $D = 0.63$ ,  $P = 1.7\text{e-}10$ ). There was apparent size truncation at Waikīkī and Hanauma Bay, but browsers in the north shore unprotected sites had larger size ranges than those in protected sites. There was evidence for scraper size truncation in Kāneʻohe Bay (Figure 10b, Kolmogorov-Smirnov test,  $D = 0.09$ ,  $P = 0.01$ ) and in Hanauma Bay (Figure 9c,  $D = 0.49$ ,  $P = 1.1\text{e-}05$ ). However, the fish in those regions had larger size ranges than in Waikīkī's unprotected site



(Figure 10d,  $D = 0.55$ ,  $P = 0.007$ ) and were scarcely observed throughout the north shore or in Waikīkī's protected site, resulting in patchy size distributions.

Measurements of functional diversity and redundancy were highly correlated with each other; reserve capacity increased mostly linearly with diversity, and protected sites tended to have higher diversity and reserve capacity than unprotected sites for grazers (Figure 11a), scrapers (Figure 11b), and browsers (Figure 11c). However, this pattern was obscured for urchins (Figure 11d), which had low diversity and reserve capacity in Kāneʻohe Bay but otherwise had similar reserve capacity and diversity across all regions and sites. Additionally, scraper diversity and reserve capacity were higher in Kāneʻohe Bay than all other regions, and protected sites in Kāneʻohe Bay still had greater diversity and reserve capacity than unprotected sites (Figure 10b). Reserve capacity was low across regions and sites, as no region or site had a functional guild with a reserve capacity greater than 0.5. Evenness and richness followed similar trends as diversity and reserve capacity (Figure 12), and grazers in Hanauma Bay and north shore regions were the only guild to have more than four species per functional guild on average (Figure 11a).

There was a significant difference in turf communities between regions, driven largely by the distinct turf communities in Kāneʻohe Bay (Figure 13; PERMANOVA, Pseudo- $F = 13.9$ ,  $R^2 = 0.17$ ,  $P = 0.001$ ). Turf in Kāneʻohe Bay had fewer members of the order Gelidiales, Rhodophyta, present than other regions, and no species from the order Corallinales (Appendix 1). While there was substantial overlap between turf communities in protected and unprotected sites at each region, Hanauma Bay was the only region in which there was no significant difference in turf communities between protected and unprotected sites (Pair-wise Permutation Test, Pseudo- $F = 1.13$ ,  $R^2 = 0.02$ ,  $P\text{-adj} = 0.99$ ).

## Discussion

Coral reefs are highly valuable coastal regions but are increasingly threatened by human impacts (Pauly et al. 2005; Newton et al. 2007; Bishop et al. 2011). However, these threats can be mitigated in part through the effective management of critical functional groups, such as herbivores (e.g. Pandolfi et al. 2011; Chung et al. 2018), which promote reef resilience and prevent algal dominance post-disturbance (Mumby et al. 2006a; Hughes et al. 2007; Rasher and Hay 2010). Here, I assessed O‘ahu’s current marine protected areas to determine whether they are effectively managing herbivore populations.

Fish and urchin biomass in field sites across O‘ahu was higher inside protected sites than outside, had higher browser, grazer, and scraper biomass, and had distinct herbivore assemblages. Additionally, protected sites had higher measures of functional diversity and redundancy for grazers, scrapers, and browsers. These findings are consistent with previous reports from Hawai‘i and elsewhere (Polunin and Roberts 1993; Russ and Alcala 1996; Friedlander et al. 2007a; Topor et al. 2019), and suggest that MPAs offer some measure of protection for O‘ahu’s herbivorous fish populations. However, much of these general trends were driven by observations from Hanauma Bay, which was the only region that had significantly greater biomass (herbivore or otherwise) inside the protected site and is also the only protected site that had a distinct herbivore assemblage when compared with its nearby unprotected sites.

Differences in herbivore population are likely not due to predation; Hanauma Bay was the only region with a significant difference in piscivore biomass between protected and unprotected sites. Additionally, grazers had higher biomass in protected sites in all regions, but scraper biomass was higher in unprotected sites in the Waikīkī and north shore regions. Protection had a substantial effect on browser biomass in the Hanauma Bay and Waikīkī regions,

where biomass was 17 and 14 times greater inside their respective protected sites. However, browser biomass was lower in the north shore protected site than the unprotected site, and browsers were scarcely observed at all in Kāneʻohe Bay. These results suggest that not all herbivore functional guilds have responded positively to protection, the magnitude of guild response depends on the region of the protected area. Protected sites in Kāneʻohe Bay, Waikīkī, and the north shore are overall not as effectively managing herbivore populations as the Hanauma Bay MLCD.

Scraper and browsers had the lowest biomass of all herbivore functional guilds in all sites, and browsers were completely absent from all but one transect in Kāneʻohe Bay. Additionally, while parrotfishes in the genus *Chlorurus* can excavate substratum when they reach a certain size (Green and Bellwood 2009), only two individuals larger than the 35cm threshold were observed during the surveys, indicating that there is limited ability for this functional guild to carry out its role. Fish in all functional guilds were small, and only 32 herbivorous fish larger than 40 cm were observed across all functional guilds, more than a third of which were observed in the Hanauma Bay protected site. Given that larger fish have a larger impact on the benthos (Bellwood and Choat 1990; Bellwood 1995; Ong and Holland 2010; Smith et al. 2010; Mouillot et al. 2014), it is likely that the functional impact of herbivores is limited by their smaller size structure throughout Oʻahu. This outcome can also impact further recruitment, as larger fish have higher fecundity and reproductive success (Berkeley et al. 2004; Birkeland and Dayton 2005; Hixon et al. 2014). Williams et al. (2008) suggested that Oʻahu has less than 3% prime spawner biomass observed in remote regions, defined as targeted species of fish greater than 70% of their maximum observed size, and thus has low population fecundity.

Therefore, small sized structure of herbivorous fishes of all functional guilds on O‘ahu may limit their ability to repopulate the reef, contributing to their low biomass across all regions and sites.

Functional redundancy for herbivorous fish functional guilds was also higher inside the protected sites, but was typically low all around O‘ahu. Reserve capacity was never greater than 0.5 across all regions and sites, suggesting that the key functional roles of herbivores are dominated by a single species (Johansson et al. 2013). While it is possible that the remaining species in each functional guilds are exploiting different functional niches than broad functional role classifications can capture (e.g. Bellwood et al. 2006; Kelly et al. 2016), low species richness and diversity in each functional guild limits the more cryptic functional diversity that these ecosystems might contain. By extension, the loss of further species on O‘ahu’s reefs could result in the loss of an already limited pool of ecosystem processes (Brandl and Bellwood 2016; D’agata et al. 2016; Thiault et al. 2017).

Urchins accounted for the most biomass in all regions but Kāne‘ohe Bay, although there was no clear relationship between protection and urchin biomass. Urchins are potential competitors for herbivorous fishes (e.g. Hay and Taylor 1985; Tootell and Steele 2016), so urchin biomass was expected to be relatively higher where herbivorous fish biomass was low (i.e. outside of the protected sites). However, this trend held true only in Waikīkī and Kāne‘ohe Bay, and while urchin functional diversity and redundancy was lower inside the protected sites at the north shore, Kāne‘ohe Bay, and Waikīkī, this was not the case for Hanauma Bay – the region with the greatest difference in herbivore assemblages inside and outside the protected site. It is possible that urchins did not respond to changes in herbivorous fish biomass because biomass is already low throughout O‘ahu; if competitor biomass is already low and differs only between protected and unprotected sites in certain cases, then responses to further reduced competition

may not be as apparent. Additionally, while urchin biomass and functional redundancy were higher in the Hanauma Bay protected site than the unprotected site, urchins still accounted for 93% of the total herbivore biomass in the unprotected site in this region.

It is also possible that urchin distributions were more influenced by habitat, as urchins tended to orient with different habitat types than the herbivorous fishes functional guilds in the ordination space. Herbivorous fishes tend to be associated with coral cover and habitat complexity (Coker et al. 2014; Jouffray et al. 2015; Yeager et al. 2017), and herbivorous fish biomass tends to be associated with more productive algal turfs (Russ 2003; Yeager et al. 2017). While urchin biomass is not associated with turf productivity (Yeager et al. 2017), and their distribution is likely influenced by settlement cues, such as the presence of certain macroalgae and biofilms (Dworjanyn and Pirozzi 2008; Mos et al. 2011), as well as post-settlement mortality (Mos et al. 2011). Habitat cues could also explain the low urchin biomass in Kāneʻohe Bay, a unique ecosystem comprised of a network of patch reefs, including Oʻahuʻs only barrier reef. It is possible that the reefs surveyed in Kāneʻohe Bay are simply less favorable habitats for urchins than the other regions. Regardless, the numerical dominance of urchins on Oʻahuʻs reefs suggests that they are likely key sources of both grazing (Hay and Taylor 1985; Mumby et al. 2006b, 2007; Sangil and Guzman 2016) and bioerosion (Carriero-Silva and McClanahan 2001; Griffin et al. 2003), and future studies should further investigate their distribution and role on Hawaiʻiʻs reefs.

While previous studies have variously emphasized the role of turf as a major source of primary productivity on coral reefs (Adey and Goertemiller 1987), as a possible threat to coral health (e.g. Carpenter 1986; Birrell et al. 2008; Vermeij et al. 2008), and as food for most herbivorous fishes (Hay and Taylor 1985; Kelly et al. 2016), this study includes a comprehensive

survey of fine-scale turf species composition on O‘ahu. Both turf and herbivore communities displayed similar trends across regions. Both turf and herbivore communities in Kāne‘ohe Bay were distinct from other regions, and there was overlap in turf and herbivore communities at all other regions. These results suggest that herbivore and turf communities are correlated with each other (Russ 2003; Yeager et al. 2017), which is consistent with previous studies indicating that fish and benthic communities reciprocally structure each other (Hixon 1986; Coker et al. 2014). However, turf communities appeared more distinct across site and region than herbivore communities, and while Hanauma Bay was the only region that had a significant difference in herbivore assemblage between its protected and unprotected site, it was also the only region that did not have a significant difference in turf assemblages. Thus, it is unclear from these results how changes in herbivore and turf community structure influence each other. Stuercke and McDermid (2004) found that turf communities are affected by physical factors such as wave exposure, and Smith et al. (2010) found that turf community composition is further altered by the interactions of time, grazing and bottom-up factors such as nutrient enrichment. By extension, differences in herbivore community may interact with the structuring impact of physical factors to drive turf community species composition. Given that herbivorous fishes are likely selective in the taxa of turf that they consume (Kelly et al. 2016) and turfs can have deleterious effects on coral reefs in the absence of grazing (Carpenter 1986; Hughes et al. 2007), it is important to understand how turfs respond to changes in herbivore assemblages. Further research should be conducted to quantify the interaction between herbivory and turf communities.

While the protected site in Hanauma Bay had healthier fish and urchin populations than the unprotected site, it is important to acknowledge the differences in habitat quality between the protected and unprotected sites. The unprotected site was in/near Maunalua Bay, which has been

impacted by years of coastal development, invasive algal dominance, and experiences large seasonal swells. Development has led to increased polluted water runoff, sedimentation, coastal erosion, and eutrophication (Wolanski et al. 2009). The protected site is in Hanauma Bay proper, which is comparatively pristine, has no substantial invasive algal growth, and experiences less runoff, sedimentation, and swell. Given that herbivore populations have been tied to habitat characteristics in this and other studies (e.g. Jouffray et al. 2015; Yeager et al. 2017), it is likely that the differences observed in these herbivore assemblages arise in part to the vast difference in habitats. This caveat is not unique to the Hanauma Bay region. The unique nature of the Kāneʻohe Bay has already been discussed, and the unprotected site in this region encompassed both the fringing reef and patch reefs spatially separated from the protected site. The Waikīkī protected site is a coastal and shallow area subject to seasonal swell and intense coastal development, whereas the unprotected colonized site is deeper and further off-shore. The north shore region had the fewest physical differences between the protected and unprotected sites, and this was the region with the smallest effect size of protection for all herbivorous fish functional guilds. These differences suggest that the efficacy of a MPA on Oʻahu should not be evaluated solely on comparisons between neighboring sites. Evaluation of future MPAs should be based on extensive survey work prior to the establishment of an MPA to allow for proper Before-After Control-Impact design as opposed to comparing neighboring sites, such as the methods used to evaluate the effectiveness of the Kahekili Herbivore Fisheries Management Area on Maui (Williams et al. 2016).

As Hawaiʻi proceeds with its goal to effectively manage 30% of its coastal zone by 2030, it is important to assess the efficacy of the current MPAs in protecting critical ecosystem processes. While herbivore biomass and functional redundancy were higher inside Oʻahu’s

protected areas, they were still low, with scrapers and browsers particularly poorly represented. These patterns indicate that O‘ahu’s current MPAs have limited effectiveness in protecting herbivore populations. While troubling, this result is consistent with previous findings that reef fishes in O‘ahu have low biomass, richness, and spawning potential (Williams et al. 2008; Gorospe et al. 2018). Additionally, evidence of poaching within the protected areas, such as the presence of line, fish with spearfishing wounds, and presence of fishermen, were observed in all regions except Hanauma Bay, suggesting limited enforcement within the MPAs. Furthermore, prior studies have found that coastal development limits MPA effectiveness (Cicin-Sain and Belfiore 2005; Suchley and Alvarez-Filip 2018), which is likely the case on O‘ahu. However, Gorospe et al. (2018) suggested that O‘ahu has a high recovery potential, and could see up to a 280% increase in fish biomass if human impacts can be managed or minimized. This emphasizes the importance of proper management, such as by increasing enforcement (e.g. Chung et al. 2018) and incorporating better land-use practices in management plans and future MPA planning (Cicin-Sain and Belfiore 2005; Suchley and Alvarez-Filip 2018). Further effort should be placed on bolstering the ecosystem function provided by these populations in O‘ahu’s current MPA network in addition to future MPAs. As the oceans continue to warm and acidify, the resilience of coral reefs will be dependent on healthy and diverse herbivore assemblages.



## Tables

**Table 1** Functional guild classifications for all herbivore/omnivore species observed during the study.

Family	Species	Functional guild	Source
Acanthuridae	<i>Naso lituratus</i>	Browser	Green and Bellwood 2009
Acanthuridae	<i>Naso unicornis</i>	Browser	Green and Bellwood 2009
Kyphosidae	<i>Kyphosus vaigiensis</i>	Browser	Green and Bellwood 2009
Scaridae	<i>Calotomus carolinus</i>	Browser	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus achilles</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus blochii</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus dussumieri</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus leucopareius</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus nigrofusus</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus nigroris</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus olivaceus</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus triostegus</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Acanthurus xanthopterus</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Ctenochaetus strigosus</i>	Grazer	Froese and Pauly 2017; Randall 2010
Acanthuridae	<i>Zebrasoma flavescens</i>	Grazer	Green and Bellwood 2009
Acanthuridae	<i>Zebrasoma veliferum</i>	Grazer	Green and Bellwood 2009
Blenniidae	<i>Cirripectes vanderbilti</i>	Grazer	Froese and Pauly 2017
Pomacanthidae	<i>Centropyge loriculus</i>	Grazer	Green and Bellwood 2009; Froese and Pauly 2017
Pomacanthidae	<i>Centropyge potteri</i>	Grazer	Green and Bellwood 2009; Froese and Pauly 2017
Tetradontidae	<i>Canthigaster amboinensis</i>	Grazer	Froese and Pauly 2017
Scaridae	<i>Chlorurus perspicillatus</i>	Scraper/excavator	Green and Bellwood 2009; Froese and Pauly 2017
Scaridae	<i>Chlorurus spilurus</i>	Scraper/excavator	Green and Bellwood 2009
Scaridae	<i>Scarus psittacus</i>	Scraper/excavator	Green and Bellwood 2009
Scaridae	<i>Scarus rubroviolaceus</i>	Scraper/excavator	Green and Bellwood 2009

**Table 1 (cont.)**

<b>Family</b>	<b>Species</b>	<b>Functional guild</b>	<b>Source</b>
Cidaridae	<i>Eucidaris metularia</i>	Urchin	N/A
Diadematidae	<i>Diadema paucispinum</i>	Urchin	N/A
Diadematidae	<i>Didadema savignyi</i>	Urchin	N/A
Diadematidae	<i>Echinothrix calamaris</i>	Urchin	N/A
Diadematidae	<i>Echinothrix diadema</i>	Urchin	N/A
Echinometridae	<i>Echinometra mathaei</i>	Urchin	N/A
Echinometridae	<i>Echinometra oblonga</i>	Urchin	N/A
Echinometridae	<i>Echinostrephus aciculatus</i>	Urchin	N/A
Echinometridae	<i>Heterocentrotus mammillatus</i>	Urchin	N/A
Toxopneustidae	<i>Tripneustes gratilla</i>	Urchin	N/A

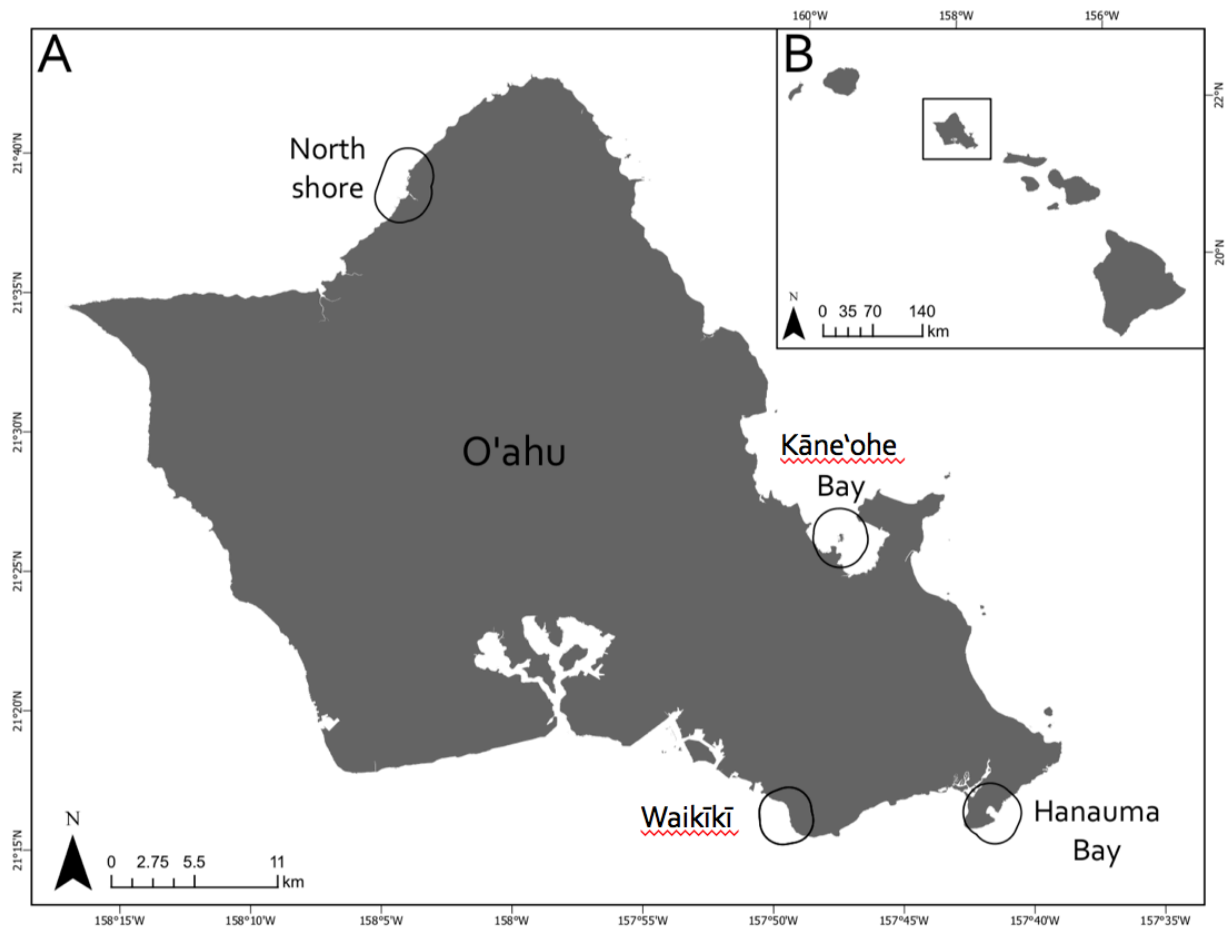
**Table 2:** Mean biomass ( $\text{g/m}^2 \pm \text{SE}$ ) for total fish and urchin biomass and each functional guild inside and outside protected sites in each region.

Region	Status	Total	Piscivore	Invertivore	Corallivore	Planktivore	Grazer	Scraper	Browser	Urchin
O'ahu	Protected	116. $\pm$ 17.5	4.83 $\pm$ 0.89	7.58 $\pm$ 1.02	0.544 $\pm$ 0.14	1.68 $\pm$ 0.39	30.1 $\pm$ 3.19	7.62 $\pm$ 1.56	7.87 $\pm$ 1.95	58.9 $\pm$ 15.4
	Unprotected	98.1 $\pm$ 10.4	2.71 $\pm$ 0.73	6.43 $\pm$ 0.97	0.488 $\pm$ 0.13	1.49 $\pm$ 0.63	16.7 $\pm$ 3.89	3.47 $\pm$ 0.96	3.82 $\pm$ 1.53	63.6 $\pm$ 9.01
Hanauma Bay	Protected	195. $\pm$ 50.5	6.99 $\pm$ 2.45	7.54 $\pm$ 0.97	0.52 $\pm$ 0.23	0.29 $\pm$ 0.14	34.8 $\pm$ 2.76	15.9 $\pm$ 4.44	7.64 $\pm$ 1.59	121. $\pm$ 48.9
	Unprotected	121. $\pm$ 25.6	1.33 $\pm$ 1.17	2.75 $\pm$ 0.97	0.16 $\pm$ 0.13	2.31 $\pm$ 2.29	6.69 $\pm$ 2.98	1.03 $\pm$ 0.52	0.45 $\pm$ 0.32	106.9 $\pm$ 22.8
Kāne'ohe Bay	Protected	28.8 $\pm$ 6.28	2.47 $\pm$ 0.76	8.5 $\pm$ 2.24	0.8 $\pm$ 0.39	4.51 $\pm$ 1.09	15.6 $\pm$ 2.77	4.26 $\pm$ 0.98	0.06 $\pm$ 0.06	1.07 $\pm$ 0.78
	Unprotected	29.4 $\pm$ 8.25	3.02 $\pm$ 1.18	6.5 $\pm$ 2.08	0.9 $\pm$ 0.33	1.31 $\pm$ 0.47	6.12 $\pm$ 1.66	3.76 $\pm$ 1.39	0 $\pm$ 0	11.4 $\pm$ 7.21
North Shore	Protected	112. $\pm$ 18.0	3.38 $\pm$ 0.85	5.98 $\pm$ 0.61	0.56 $\pm$ 0.21	0.56 $\pm$ 0.18	24.8 $\pm$ 2.52	5.00 $\pm$ 2.1	8.93 $\pm$ 3.54	62.4 $\pm$ 15.0
	Unprotected	87.5 $\pm$ 15.1	5.11 $\pm$ 2.25	11.8 $\pm$ 2.79	0.71 $\pm$ 0.34	2.18 $\pm$ 1.01	20.9 $\pm$ 4.85	5.84 $\pm$ 3.17	13.3 $\pm$ 5.69	27.6 $\pm$ 5.81
Waikīkī	Protected	144. $\pm$ 32.3	8.14 $\pm$ 2.79	9.05 $\pm$ 5.27	0.04 $\pm$ 0.04	1.02 $\pm$ 0.6	60.5 $\pm$ 17.2	2.91 $\pm$ 1.48	21.8 $\pm$ 10.2	42.9 $\pm$ 6.87
	Unprotected	154. $\pm$ 20.6	1.39 $\pm$ 0.81	4.68 $\pm$ 0.55	0.18 $\pm$ 0.1	0.17 $\pm$ 0.09	32.9 $\pm$ 13.8	3.24 $\pm$ 1.58	1.51 $\pm$ 0.35	108.5 $\pm$ 18.1

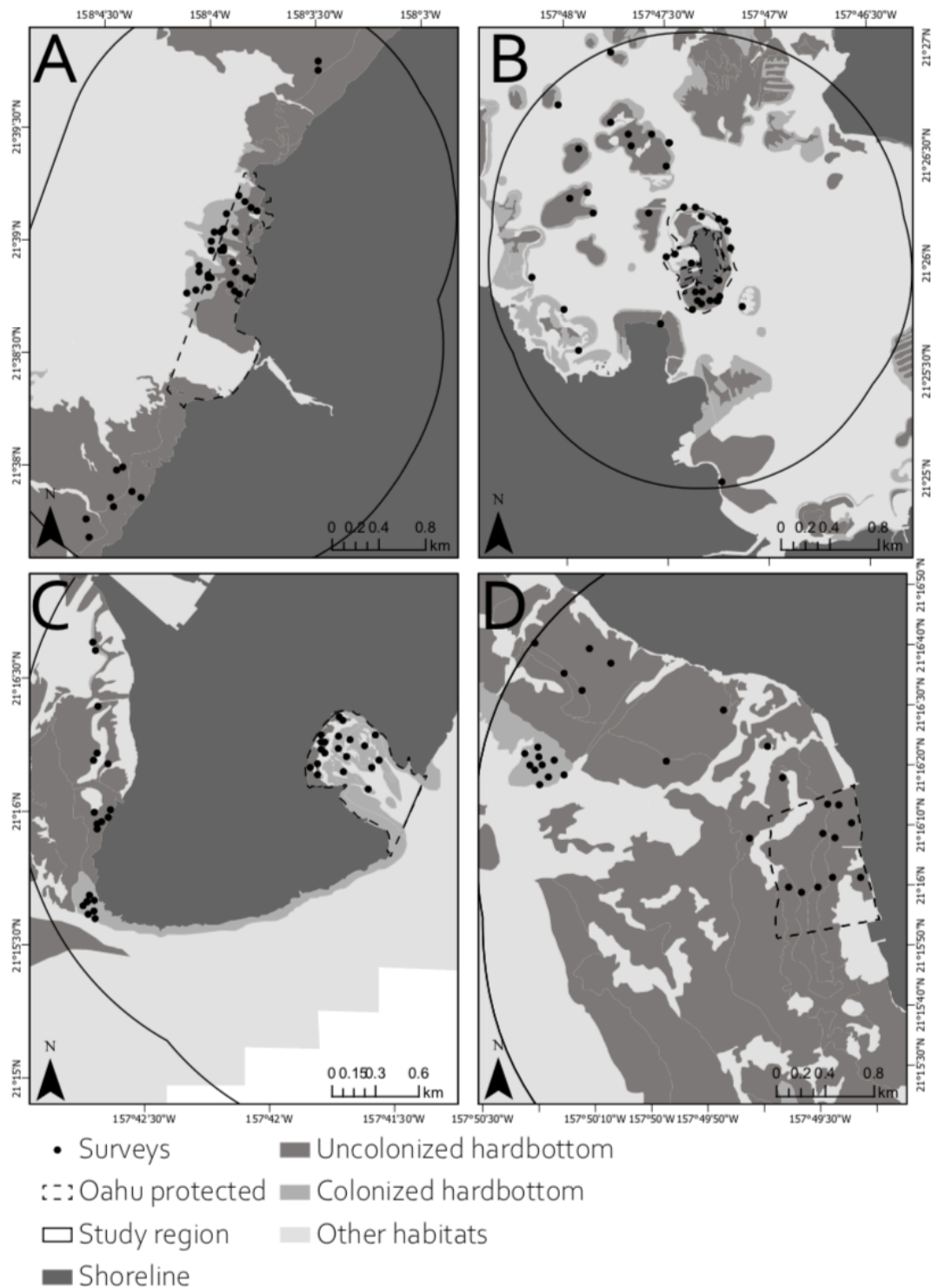
**Table 3:** Ratio of the biomass inside protected sites to outside protected sites in each region for total biomass (fishes and urchins), combined herbivores, piscivores, and the individual herbivore functional guilds.

Total (Fish and urchins)		Piscivores	Herbivores	Grazer	Scraper	Browser	Urchin
Oahu							
Average	1.2	1.8	1.2	1.8	2.2	2.1	0.9
Hanauma	1.6	5.3	1.6	5.2	15.4	17.0	1.1
Kāneʻohe	1.2	0.8	1.0	2.5	1.1	NA	0.1
North shore	1.3	0.7	1.5	1.2	0.9	0.7	2.3
Waikīkī	0.9	5.9	0.9	1.8	0.9	14.4	0.4

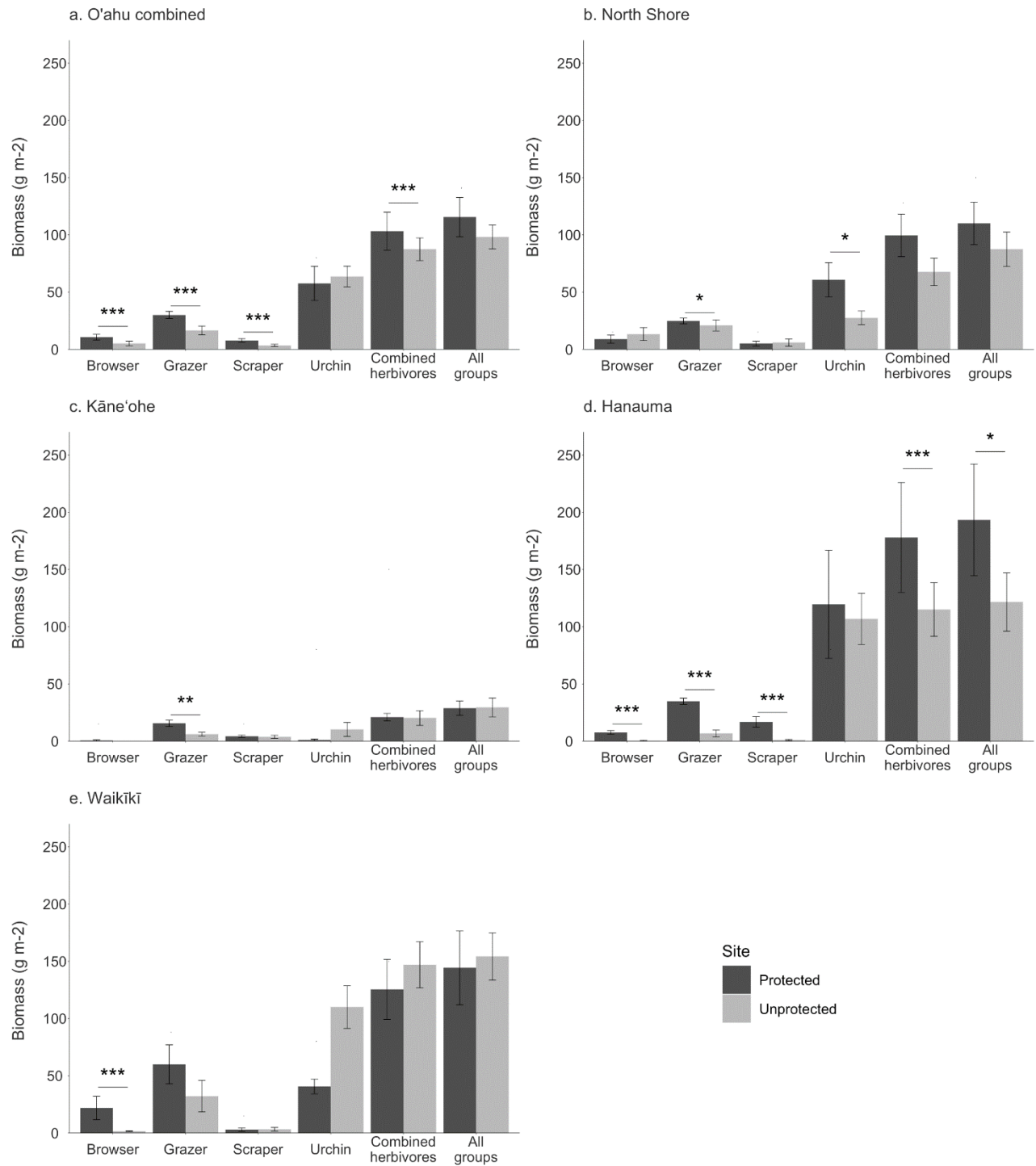
## Figures



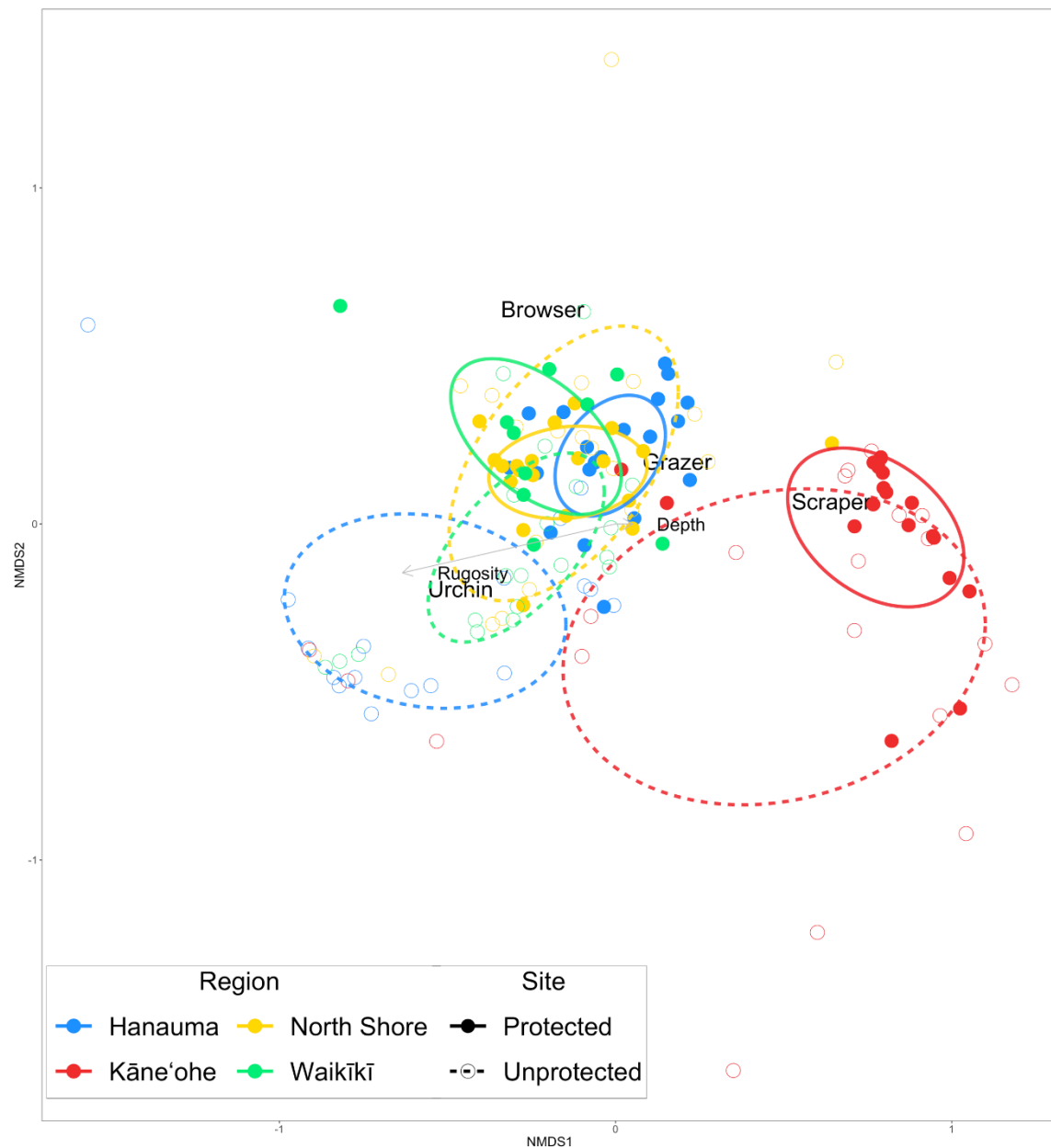
**Figure 1** Map of a) O'ahu in b) the Main Hawaiian Islands, where study regions are bounded by bold lines



**Figure 2:** Map of a) the north shore study region, b) the Kāneʻohe Bay study region, c) the Hanauma Bay study region, and d) the Waikīkī study region. Protected sites are bounded by dashed lines and the buffer for unprotected sites is bounded by bold lines. Colonized and uncolonized hardbottom are represented by light and dark grey, respectively. Land is represented by the darkest grey. Survey coordinates are marked with black points

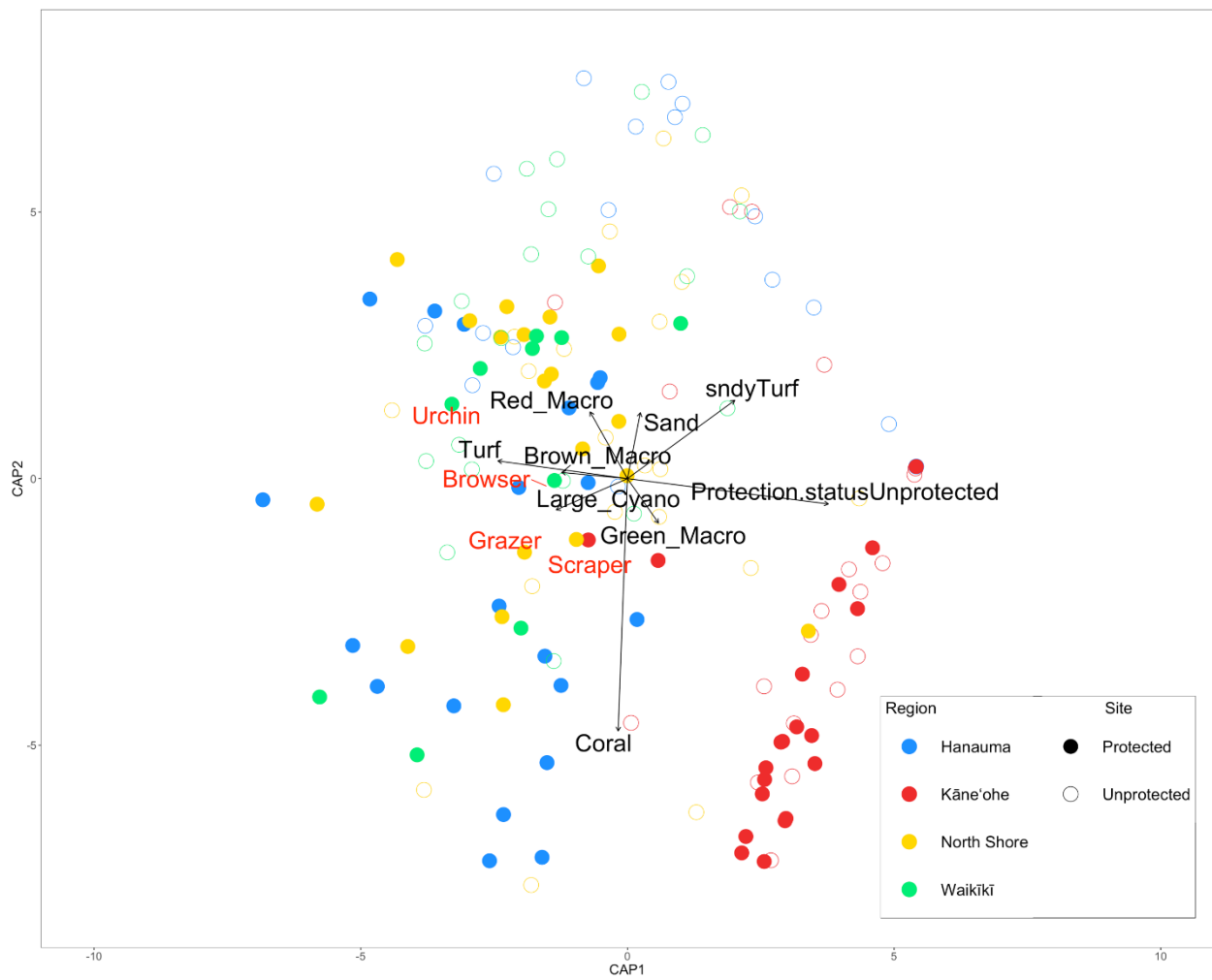


**Figure 3:** Mean biomass ( $\pm$  SE) of herbivore functional guilds, mean total herbivore biomass ( $\pm$  SE), and mean total biomass ( $\pm$  SE) including non-herbivores inside and outside protected areas (a) across all regions in O'ahu, (b) off the north shore, (c) in Kāne'ohe Bay, (d) in Hanauma Bay, and (e) off Waikīkī. \* indicates statistical significance ( \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001).

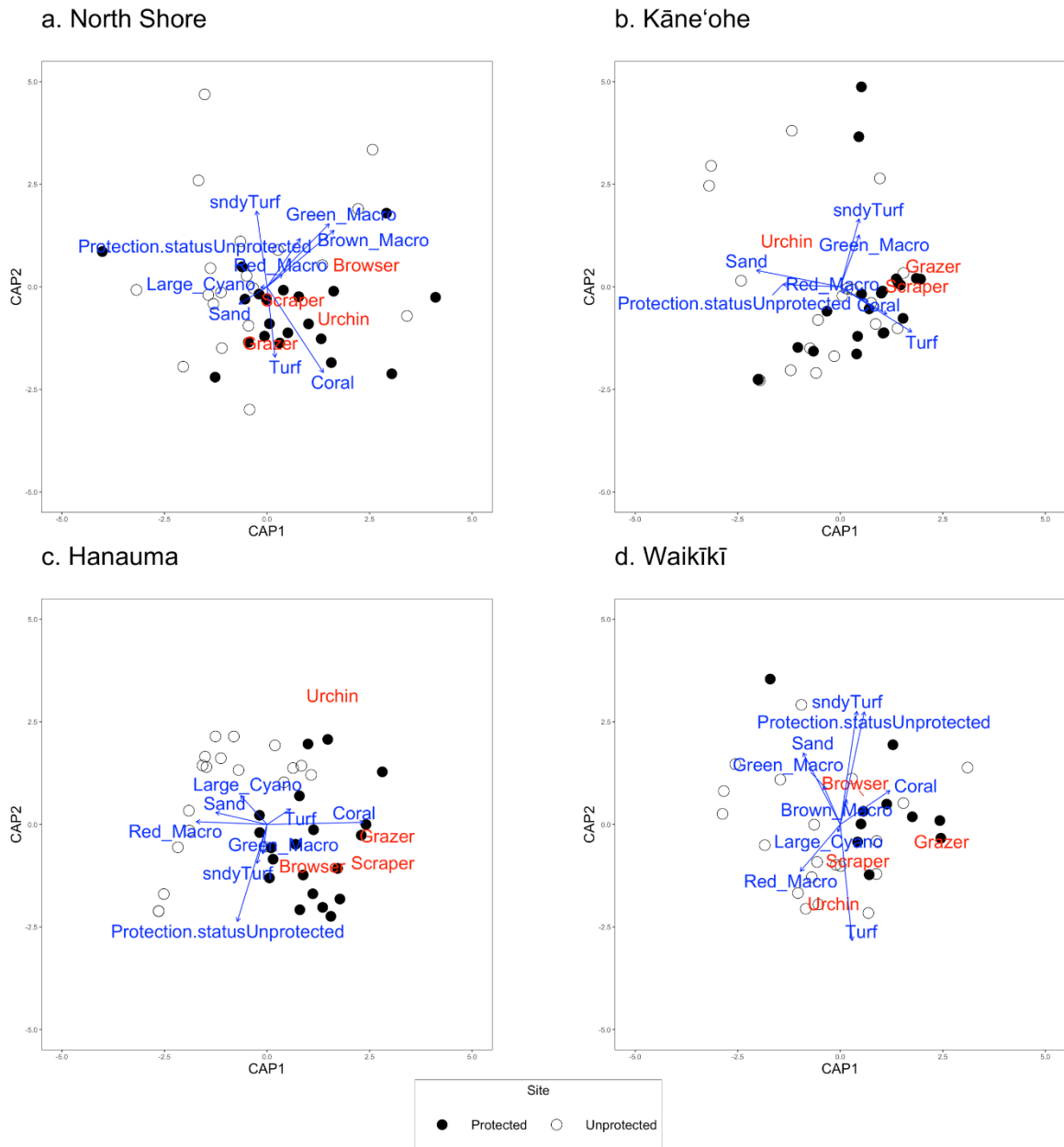


**Figure 4:** Multivariate comparison of biomass with an nMDS plot of herbivore communities around O'ahu based on  $\log(\text{biomass} + 1)$ . Color indicates region (blue = Hanauma Bay, red = Kāne'ohe Bay, yellow = north shore, green = Waikīkī) and shape indicates site (solid = protected sites, open = unprotected sites). Bold ellipses bound protected sites and dashed ellipses bound unprotected sites.

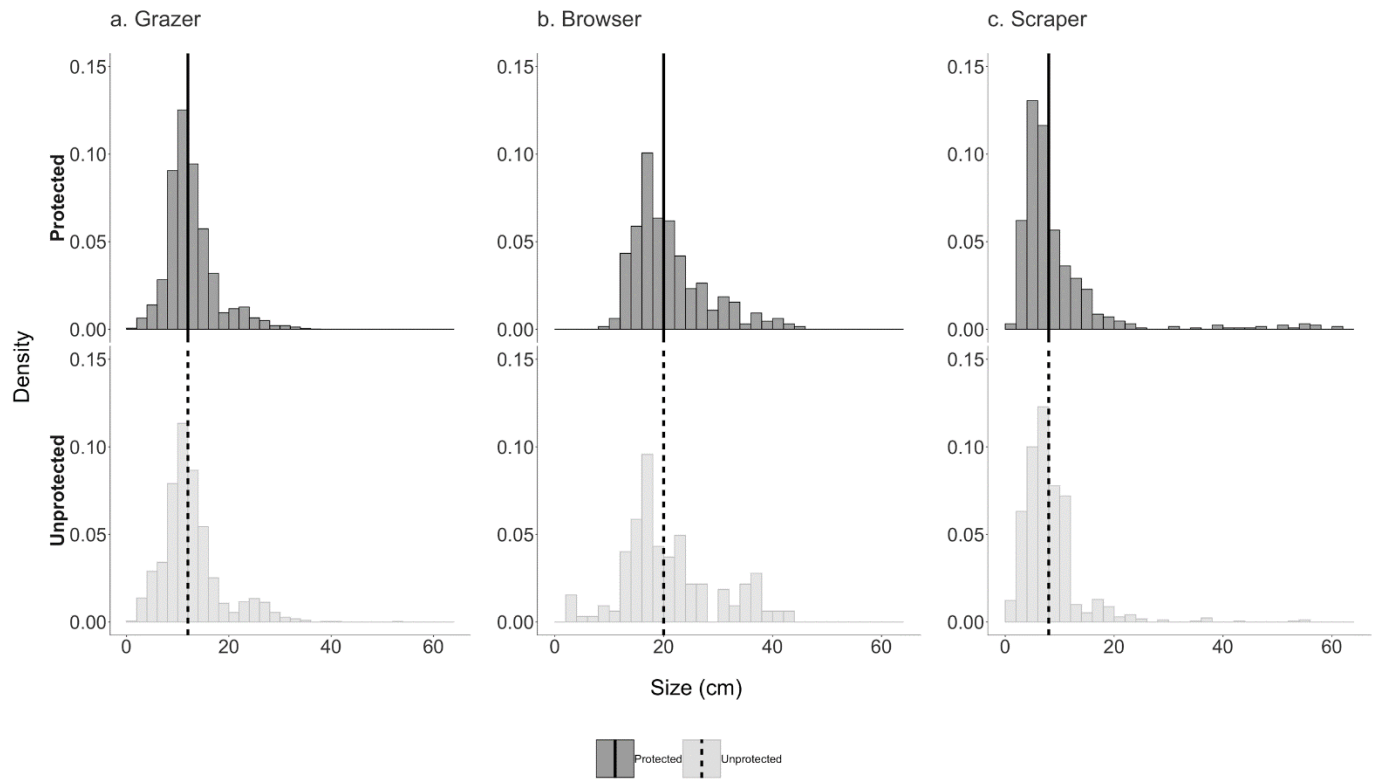




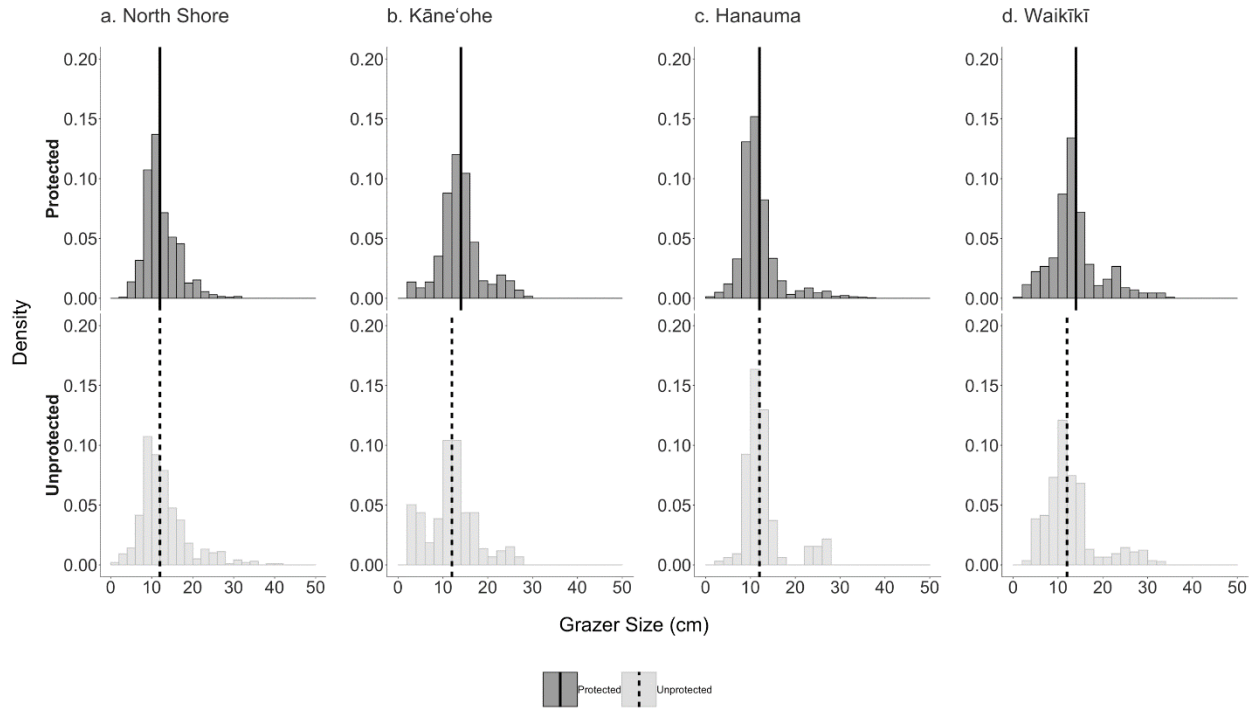
**Figure 5:** Constrained ordination using a canonical analysis of principal components of herbivore communities around O'ahu with protection status and benthic community as predictors. Color indicates the region (blue = Hanauma Bay, red = Kāne'ohe Bay, yellow = north shore, green = Waikīkī) and shape indicates site (solid = protected sites, open = unprotected sites). Length of the loadings is proportional to the amount of variation explained in the constrained axes.



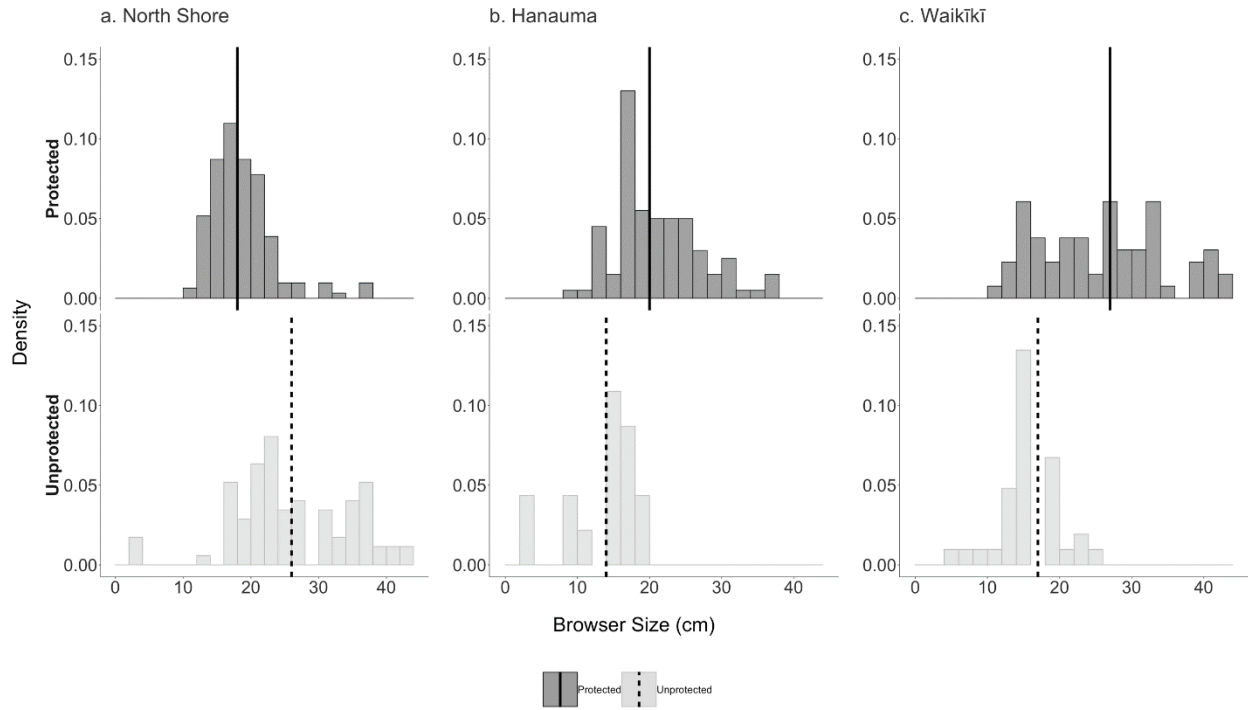
**Figure 6:** Constrained ordination using a canonical analysis of principal components (CAP) of (a) north shore, (b) Kāneʻohe Bay, (c) Hanauma Bay, and (d) Waikīkī herbivore communities with protection status and benthic community as predictors. Shape indicates site (solid = protected sites, open = unprotected sites). Text color indicates community data (Red = herbivore community, blue = benthic community). Length of the loadings is proportional to the amount of variation explained in the constrained axes.



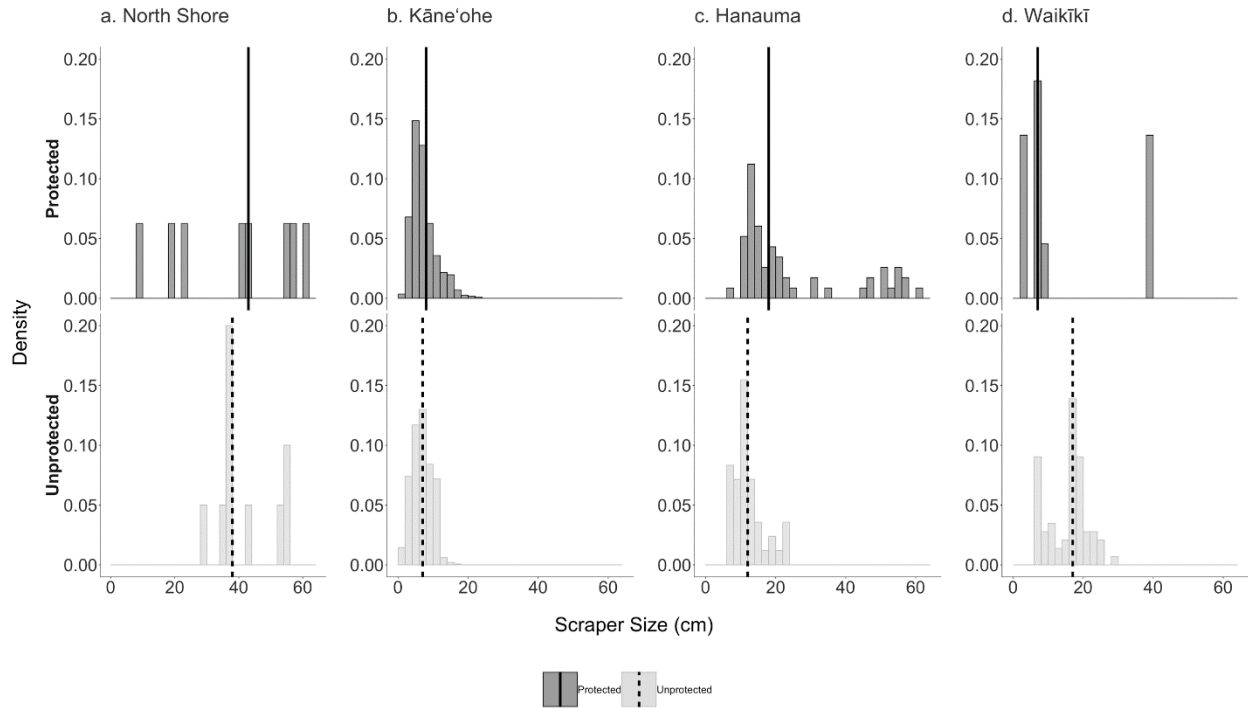
**Figure 7:** Size distributions of (a) grazers, (b) browsers, and (c) scraper herbivorous fishes across all regions around O‘ahu. Darker histograms in the top row represent size distributions in protected sites and lighter histograms in the bottom row represent size distributions in unprotected sites. Bold lines represent median size in protected sites and dashed lines represent median size in unprotected sites.



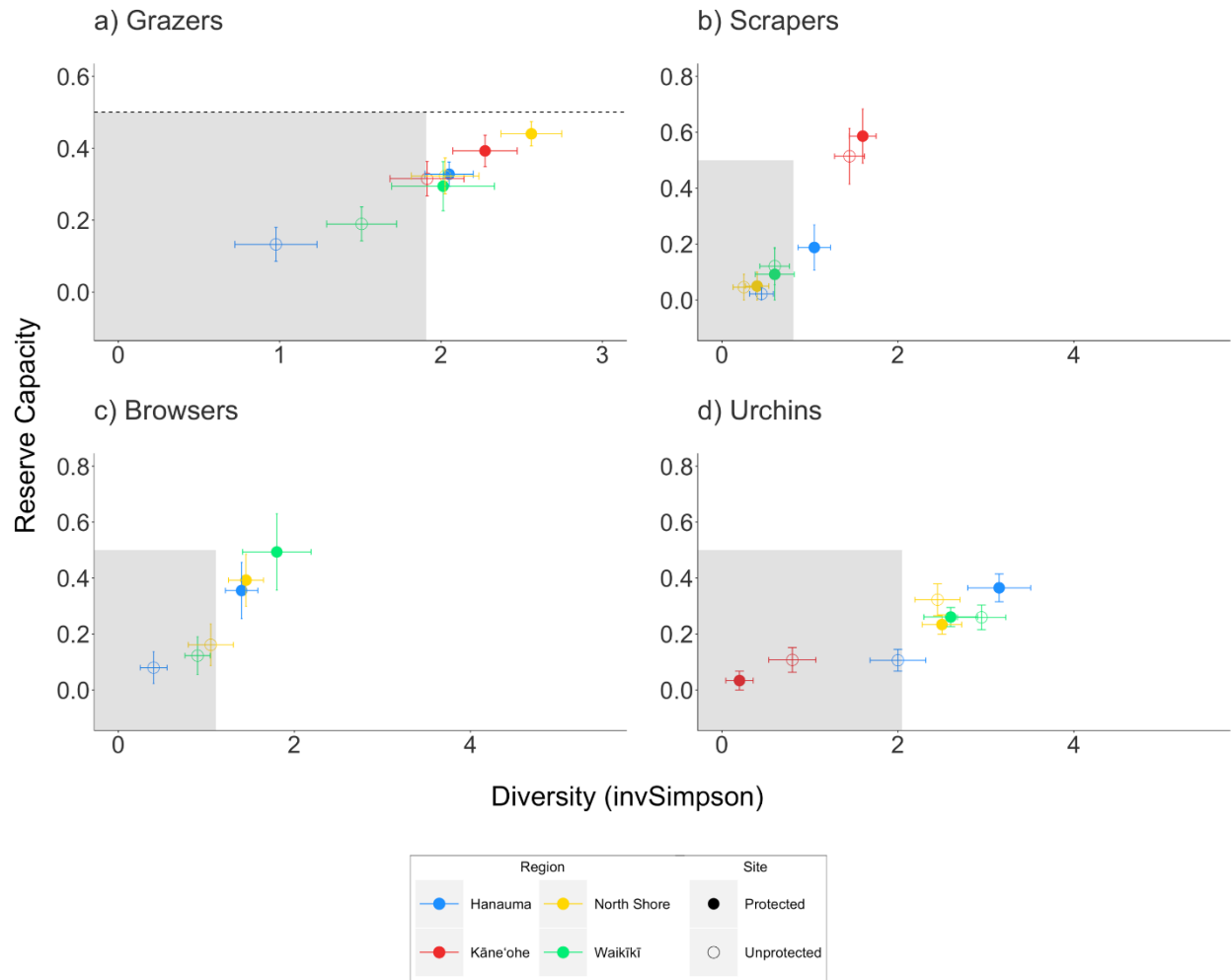
**Figure 8:** Grazer size distributions at (a) the north shore, (b) Kāneʻohe Bay, (c) Hanauma Bay, and (d) Waikīkī regions. Darker histograms in the top row represent size distributions in protected sites and lighter histograms in the bottom row represent size distributions in unprotected sites. Bold lines represent median size in protected sites and dashed lines represent median size in unprotected sites.



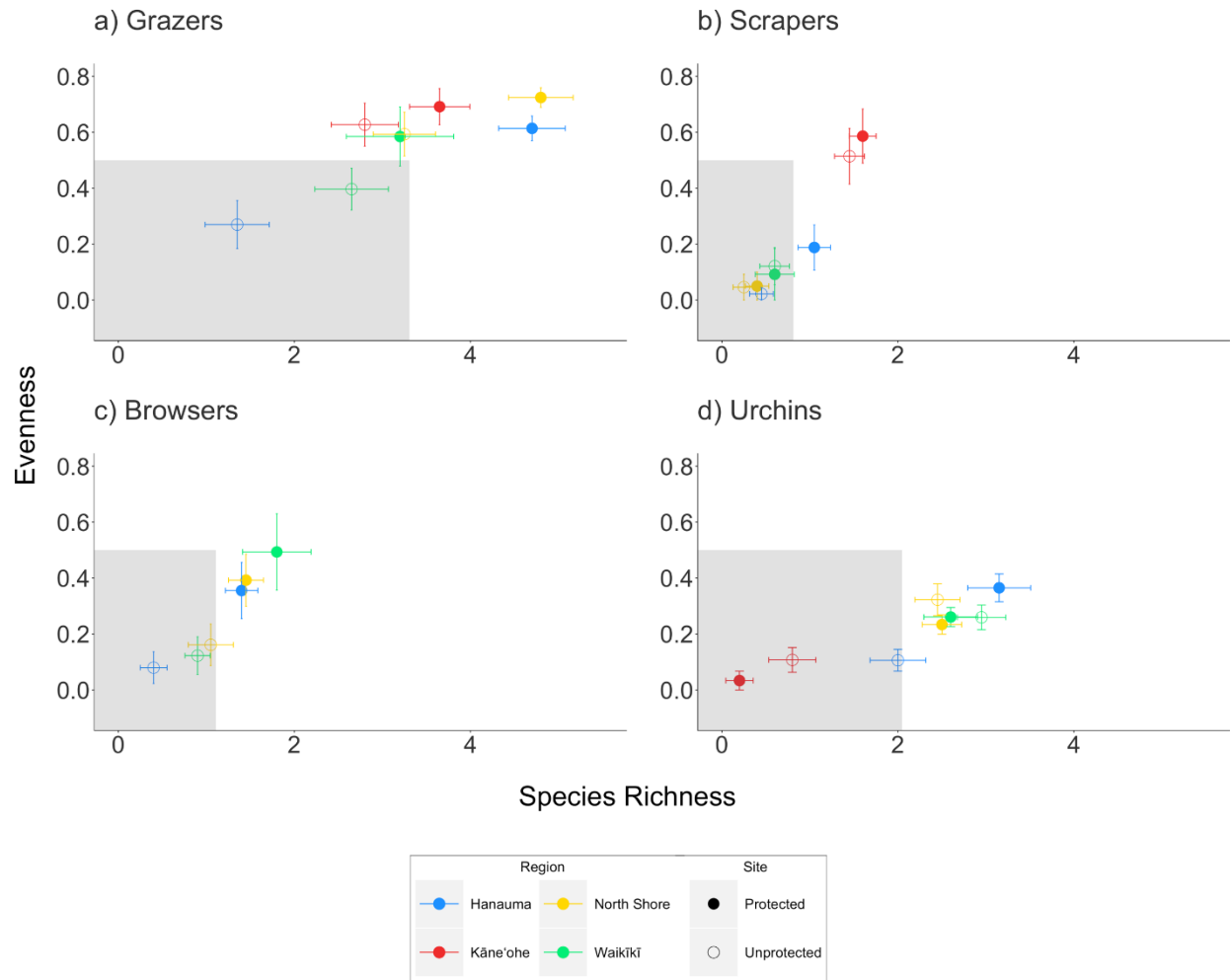
**Figure 9:** Browser size distributions at (a) the north shore, (b) Kāneʻohe Bay, (c) Hanauma Bay, and (d) Waikīkī regions. Darker histograms in the top row represent size distributions in protected sites and lighter histograms in the bottom row represent size distributions in unprotected sites. Bold lines represent median size in protected sites and dashed lines represent median size in unprotected sites.



**Figure 10:** Scraper size distributions at (a) the north shore, (b) Kāneʻohe Bay, (c) Hanauma Bay, and (d) Waikīkī regions. Darker histograms in the top row represent size distributions in protected sites and lighter histograms in the bottom row represent size distributions in unprotected sites. Bold lines represent median size in protected sites and dashed lines represent median size in unprotected sites.

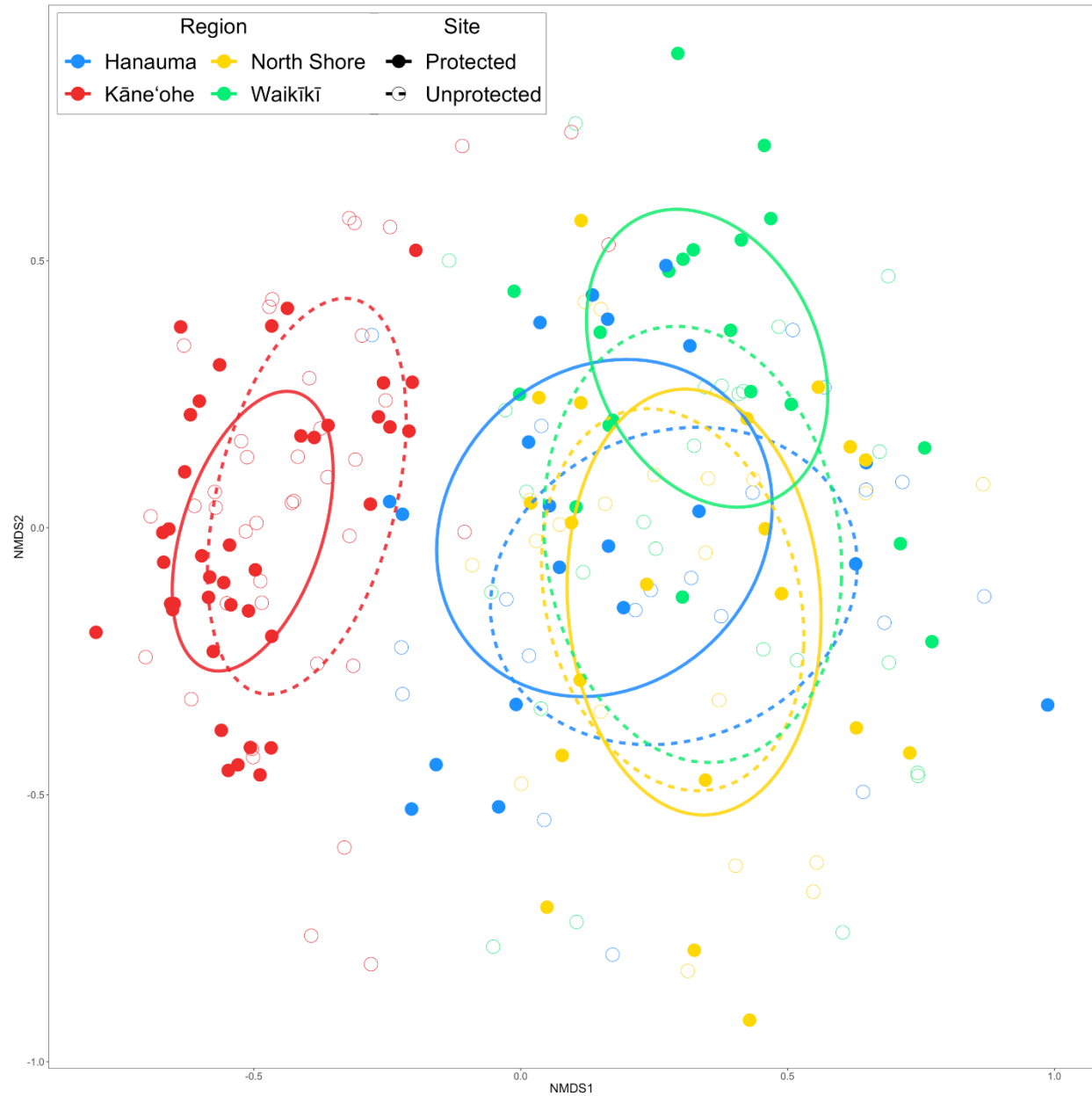


**Figure 11:** Mean Reserve Capacity and diversity (invSimpsons) ( $\pm$  SE) for four functional guilds of herbivores: (a) grazers, (b) scrapers, (c) browsers, and (d) urchins across protected/unprotected sites in the four study regions. Color indicates region (blue = Hanauma Bay, red = Kāneʻohe Bay, yellow = north shore, green = Waikīkī) and shape indicates site (solid = protected sites, open = unprotected sites). The dashed line represents reserve capacity  $< 0.5$ , indicating low functional redundancy, and the shaded area of the graph represents below average diversity.



**Figure 12:** Mean evenness and species richness ( $\pm$  SE) for four functional guilds of herbivores: (a) grazers, (b) scrapers, (c) browsers, and (d) urchins across protected/unprotected regions in the four study regions. Color indicates region (blue = Hanauma Bay, red = Kāne'ohe Bay, yellow = north shore, green = Waikīkī) and shape indicates site (solid = protected sites, open = unprotected sites). The shaded area of the graph represents below average evenness and richness.





**Figure 13:** nMDS plot of turf communities around O‘ahu. Color indicates region (blue = Hanauma Bay, red = Kāne‘ohe Bay, yellow = north shore, green = Waikīkī) and shape indicates site (solid = protected sites, open = unprotected sites). Bold ellipses bound protected sites and dashed ellipses bound unprotected sites.

## Appendices

**Appendix 1:** Test statistics from GLM Two-Way ANOVAs assessing differences in Reserve Capacity, Diversity, Evenness, and Richness between regions and protected sites around O‘ahu.

Measure	Guild	Source	$\chi^2$	df	P
Reserve Capacity	Grazer	Protection	14.7	1	0.0001
		Region	16.8	3	0.0007
		Interaction	1.9	3	0.59
	Scraper	Protection	1.9	1	0.16
		Region	50.9	3	4.90E-05
		Interaction	1.88	3	0.59
	Browser	Protection	14.4	1	1.50E-04
		Region	0.5	2	0.8
		Interaction	2.14	2	0.34
	Urchin	Protection	0.9	1	0.34
		Region	17.8	3	4.70E-04
		Interaction	25.7	3	1.10E-05
Diversity	Grazer	Protection	16.4	1	5.10E-05
		Region	15.8	3	0.001
		Interaction	3.4	3	0.35
	Scraper	Protection	4.9	1	3.00E-02
		Region	61.8	3	4.25E-13
		Interaction	3.21	3	0.36
	Browser	Protection	20.6	1	6.77E-06
		Region	3.55	2	0.17
		Interaction	3.74	2	0.15
	Urchin	Protection	0.08	1	0.77
		Region	136	3	2.22E-16
		Interaction	19.2	3	2.50E-04
Evenness	Grazer	Protection	12.8	1	3.30E-04
		Region	15.8	3	0.001
		Interaction	4.55	3	0.21
	Scraper	Protection	1.34	1	0.25
		Region	63.4	3	1.10E-13
		Interaction	1.98	3	0.58
	Browser	Protection	16	1	6.30E-05
		Region	0.87	2	0.65
		Interaction	0.59	2	0.74
	Urchin	Protection	0.69	1	0.4
		Region	29.2	3	1.90E-06
		Interaction	21.1	3	9.90E-05

**Appendix 1 (cont.)**

Richness	Grazer	Protection	35.9	1	2.08E-09
		Region	8.69	3	0.03
		Interaction	15.3	3	0.001
	Scraper	Protection	4.65	1	0.03
		Region	65.9	3	5.19E-14
		Interaction	3.88	3	0.27
	Browser	Protection	18.8	1	1.44E-05
		Region	4.75	2	0.09
		Interaction	2.51	2	0.29
	Urchin	Protection	0.25	1	0.61
		Region	92.6	3	2.20E-16
		Interaction	12	3	0.007

**Appendix 2:** Mean reserve capacity (RC), diversity (invSimpsons), species richness, and evenness across regions and sites for each functional guild ( $\pm$ SE).

			RC	Diversity	Richness	Evenness
Grazers	Hanauma	Protected	0.33 $\pm$ 0.03	2.05 $\pm$ 0.15	4.7 $\pm$ 0.38	0.61 $\pm$ 0.04
	Hanauma	Unprotected	0.13 $\pm$ 0.05	0.98 $\pm$ 0.25	1.35 $\pm$ 0.36	0.27 $\pm$ 0.09
	Kaneohe	Protected	0.39 $\pm$ 0.04	2.27 $\pm$ 0.2	3.65 $\pm$ 0.34	0.69 $\pm$ 0.06
	Kaneohe	Unprotected	0.32 $\pm$ 0.05	1.91 $\pm$ 0.23	2.8 $\pm$ 0.38	0.63 $\pm$ 0.08
	North Shore	Protected	0.44 $\pm$ 0.03	2.56 $\pm$ 0.19	4.8 $\pm$ 0.37	0.72 $\pm$ 0.04
	North Shore	Unprotected	0.32 $\pm$ 0.05	2.03 $\pm$ 0.21	3.25 $\pm$ 0.35	0.59 $\pm$ 0.08
	Waikiki	Protected	0.29 $\pm$ 0.07	2.01 $\pm$ 0.32	3.2 $\pm$ 0.61	0.58 $\pm$ 0.11
	Waikiki	Unprotected	0.19 $\pm$ 0.05	1.51 $\pm$ 0.22	2.65 $\pm$ 0.42	0.4 $\pm$ 0.07
Browsers	Hanauma	Protected	0.15 $\pm$ 0.05	1.29 $\pm$ 0.16	1.4 $\pm$ 0.18	0.36 $\pm$ 0.1
	Hanauma	Unprotected	0.03 $\pm$ 0.03	0.37 $\pm$ 0.14	0.4 $\pm$ 0.15	0.08 $\pm$ 0.06
	North Shore	Protected	0.14 $\pm$ 0.04	1.2 $\pm$ 0.15	1.45 $\pm$ 0.2	0.39 $\pm$ 0.09
	North Shore	Unprotected	0.07 $\pm$ 0.03	0.87 $\pm$ 0.18	1.05 $\pm$ 0.26	0.16 $\pm$ 0.07
	Waikiki	Protected	0.22 $\pm$ 0.07	1.39 $\pm$ 0.28	1.8 $\pm$ 0.39	0.49 $\pm$ 0.14
	Waikiki	Unprotected	0.04 $\pm$ 0.02	0.84 $\pm$ 0.12	0.9 $\pm$ 0.14	0.12 $\pm$ 0.07
Scrapers	Hanauma	Protected	0.08 $\pm$ 0.04	0.92 $\pm$ 0.14	1.05 $\pm$ 0.18	0.19 $\pm$ 0.08
	Hanauma	Unprotected	0 $\pm$ 0	0.41 $\pm$ 0.12	0.45 $\pm$ 0.14	0.02 $\pm$ 0.02
	Kaneohe	Protected	0.22 $\pm$ 0.04	1.4 $\pm$ 0.14	1.6 $\pm$ 0.15	0.59 $\pm$ 0.1
	Kaneohe	Unprotected	0.19 $\pm$ 0.04	1.28 $\pm$ 0.15	1.45 $\pm$ 0.17	0.51 $\pm$ 0.1
	North Shore	Protected	0.03 $\pm$ 0.03	0.4 $\pm$ 0.13	0.4 $\pm$ 0.13	0.05 $\pm$ 0.05
	North Shore	Unprotected	0.02 $\pm$ 0.02	0.24 $\pm$ 0.12	0.25 $\pm$ 0.12	0.05 $\pm$ 0.05
	Waikiki	Protected	0.03 $\pm$ 0.03	0.58 $\pm$ 0.21	0.6 $\pm$ 0.22	0.09 $\pm$ 0.09
	Waikiki	Unprotected	0.04 $\pm$ 0.02	0.54 $\pm$ 0.14	0.6 $\pm$ 0.17	0.12 $\pm$ 0.07
Urchins	Hanauma	Protected	0.16 $\pm$ 0.04	1.4 $\pm$ 0.09	3.15 $\pm$ 0.36	0.37 $\pm$ 0.05
	Hanauma	Unprotected	0.03 $\pm$ 0.01	0.92 $\pm$ 0.09	2 $\pm$ 0.32	0.11 $\pm$ 0.04
	Kaneohe	Protected	0.01 $\pm$ 0.01	0.13 $\pm$ 0.1	0.2 $\pm$ 0.16	0.03 $\pm$ 0.03
	Kaneohe	Unprotected	0.03 $\pm$ 0.01	0.42 $\pm$ 0.13	0.8 $\pm$ 0.27	0.11 $\pm$ 0.04
	North Shore	Protected	0.06 $\pm$ 0.01	1.09 $\pm$ 0.06	2.5 $\pm$ 0.22	0.23 $\pm$ 0.03
	North Shore	Unprotected	0.11 $\pm$ 0.03	1.17 $\pm$ 0.11	2.45 $\pm$ 0.26	0.32 $\pm$ 0.06
	Waikiki	Protected	0.06 $\pm$ 0.01	1.14 $\pm$ 0.02	2.6 $\pm$ 0.31	0.26 $\pm$ 0.03
	Waikiki	Unprotected	0.08 $\pm$ 0.02	1.2 $\pm$ 0.04	2.95 $\pm$ 0.28	0.26 $\pm$ 0.04

**Appendix 3:** Turf species identified inside and outside the protected areas.

	North Shore Protected	North Shore Unprotected	Kāneʻohe Protected	Kāneʻohe Unprotected	Hanauma Protected	Hanauma Unprotected	Waikīkī Protected	Waikīkī Unprotected
<b>Cyanobacteria</b>								
<i>Anabaena</i> sp.			X	X				
<i>Calothrix</i> sp.	X	X	X	X	X			X
<i>Lyngbya</i> sp.	X	X	X	X	X	X	X	X
<i>Oscillatoria</i> sp.		X	X	X	X	X	X	
Cyanobacteria with polar heterocyst			X	X	X		X	X
<b>Brown Algae</b>								
<i>Asteronema rhodochoortonoides</i>				X				
<i>Dictyota</i> sp.	X	X			X	X	X	X
<i>Feldmannia indica</i>				X	X	X		X
<i>Feldmannia lebelii</i>			X	X	X			X
<i>Feldmannia mitchelliae</i>							X	
<i>Feldmannia</i> sp.	X		X	X	X	X		X
<i>Kuetzingiella elachistaeformis</i>				X				
<i>Padina</i> sp.	X	X			X	X	X	X
<i>Sphacelaria novae-hollandinae</i>		X	X	X	X		X	X
<i>Sphacelaria rigidula</i>	X	X		X	X			X
<i>Sphacelaria tribuloides</i>				X				
<i>Sphacelaria</i> sp.	X	X	X	X	X	X	X	X
<i>Asteronema</i> sp			X	X				
Ectocarpales with unilocular structures								X
Uniseriate brown with anomalously swollen sides to cells that alternate from one side of the cell to the other	X	X						

Phaeophyte unknown possible Ectocarpales								
<b>Green Algae</b>								
<i>Chaetomorpha</i> sp.			X	X				
<i>Chlorodesmis caespitosa</i>					X	X		X
<i>Cladophora fuliginosa</i>		X			X			
<i>Cladophora sericea</i>	X			X			X	X
<i>Cladophora</i> sp. A			X		X			
<i>Cladophora</i> sp. B	X		X					
<i>Cladophora</i> sp. D			X				X	
<i>Cladophora</i> sp. C	X				X	X	X	X
<i>Cladophoropsis</i> <i>membranacea</i>							X	
<i>Cladophoropsis</i> sp.			X					
<i>Derbesia fastigiata</i>			X	X				
<i>Derbesia</i> sp.	X	X	X	X	X	X	X	X
<i>Rhipidosiphon</i> sp.					X	X	X	X
<i>Siphonogramen</i> <i>abbreviatum</i>	X		X			X		
<i>Siphonogramen parva</i>			X	X	X			X
<i>Ulva clathrata</i>							X	
<i>Ulva flexuosa</i>				X	X			
<i>Ulva paradoxa</i>			X	X	X		X	X
<i>Ulvella</i> sp.			X					
<i>Uronema marinum</i>	X	X	X	X	X	X	X	X
Unidentified Bryopsidaceae			X					
Laterally branching siphonous Bryopsidales			X					
Uniseriate unbranched Cladophorales sp. A			X	X			X	X
Uniseriate unbranched Cladophorales sp. B	X	X	X	X	X	X		X
Uniseriate unbranched Cladophorales sp. C			X	X				

Uniseriate unbranched Cladophorales sp. D			X		X	X		X
<b>Red Algae</b>								
<i>Aglaothamnion boergesenii</i>				X				
<i>Amansia glomerata</i>		X						
<i>Anotrichium tenue</i>	X	X		X	X	X		X
<i>Anotrichium</i> sp							X	
<i>Antithamnion percurrans</i>							X	
<i>Asparagopsis taxiformis</i>	X	X			X	X	X	X
<i>Caulacanthus ustulatus</i>					X		X	X
<i>Centroceras</i> sp	X	X		X	X	X	X	X
<i>Ceramium aduncum</i>						X		
<i>Ceramium cingulum</i>		X				X		
<i>Ceramium clarionensis</i>	X							X
<i>Ceramium codii</i>	X	X			X	X	X	X
<i>Ceramium diaphanum</i>					X	X		X
<i>Ceramium dumosertum</i>		X				X	X	
<i>Ceramium macilentum</i>				X	X		X	X
<i>Ceramium paniculatum</i>							X	
<i>Ceramium punctiforme</i>	X							
<i>Ceramium serpens</i>	X	X			X	X	X	X
<i>Ceramium vagans</i>						X	X	
<i>Ceramium womersleyi</i>							X	
<i>Ceramium</i> sp. A			X	X			X	X
<i>Ceramium</i> sp. B						X		
<i>Ceramium</i> sp. C							X	
<i>Ceratodictyon intricatum</i>	X			X				
<i>Ceratodictyon variabile</i>	X			X	X		X	
<i>Ceratodictyon</i> sp.	X	X	X		X			X
<i>Champia parvula</i>		X				X		X
<i>Chondria polyrhiza</i>	X	X				X	X	X
<i>Chondria simpliciuscula</i>	X	X			X	X	X	X
<i>Chondria</i> sp. A							X	
<i>Chondria</i> sp. B	X	X			X	X		X

<i>Chondria</i> -like									
Rhodomelaceae		X							
<i>Corallophila</i> sp.					X		X	X	
<i>Dasya</i> sp.						X	X		
<i>Digenea cymatophila</i>	X	X						X	
<i>Exophyllum wentii</i>			X						
<i>Gayliella fimbriata</i>		X		X		X	X	X	
<i>Gayliella flaccida</i>	X	X		X	X	X		X	
<i>Gelidiella acerosa</i>		X							
<i>Gelidiella</i> sp.	X	X		X	X	X			
<i>Gelidium pusillum</i>	X	X			X	X	X	X	
<i>Griffithsia heteromorpha</i>	X	X	X	X	X	X	X	X	
<i>Gymnothamnion elegans</i>									X
<i>Herposiphonia arcuata</i>							X		
<i>Herposiphonia crassa</i>						X	X		X
<i>Herposiphonia delicatula</i>		X		X	X		X		X
<i>Herposiphonia nuda</i>	X	X	X			X	X		X
<i>Herposiphonia obscura</i>							X		X
<i>Herposiphonia pacifica</i>				X	X	X	X		
<i>Herposiphonia parca</i>				X					X
<i>Herposiphonia secunda</i>	X		X		X	X			
<i>Herposiphonia variabilis</i>	X	X	X		X	X			
<i>Herposiphonia</i> sp. A				X					
<i>Herposiphonia</i> sp. B			X						
<i>Herposiphonia</i> sp. C							X		
<i>Heterosiphonia crispella</i>				X					
<i>Hypnea</i> sp.	X	X			X	X	X		X
<i>Hypoglossum minimum</i>		X							
<i>Jania adhaerens</i>	X	X			X	X	X		X
<i>Jania micrarthrodia</i>	X	X			X	X	X		X
<i>Jania pumila</i>	X	X			X	X	X		X



<i>Jania</i> sp.					X			
<i>Kapraunia pentamera</i>	X							X
<i>Lejolisia pacifica</i>	X	X	X		X	X		X
<i>Lejolisia</i> sp.			X	X				
<i>Lomentaria hakodatensis</i>	X							
<i>Lophosiphonia cristata</i>	X	X				X		X
<i>Melanothamnus apiculatus</i>	X	X			X	X		
<i>Melanothamnus delicatulus</i>	X	X				X	X	
<i>Melanothamnus pseudovillum</i>								X
<i>Melanothamnus savatieri</i>		X						
<i>Melanothamnus sparsus</i>	X	X	X		X	X		X
<i>Melanothamnus sphaerocarpus</i>		X			X	X	X	X
<i>Melanothamnus upolensis</i>		X				X		X
<i>Millerella myrioclada</i>	X			X	X	X	X	X
<i>Neosiphonia sertularioides</i>	X				X	X		
<i>Palisada crustiformans</i>		X						
<i>Polysiphonia anomala</i>	X	X	X	X	X			
<i>Polysiphonia exilis</i>	X					X		
<i>Polysiphonia homoia</i>	X							
<i>Polysiphonia howei</i>	X	X				X		X
<i>Polysiphonia profunda</i>	X					X		
<i>Polysiphonia rubrorhiza</i>			X					
<i>Polysiphonia scopulorum</i>	X	X			X	X		
<i>Polysiphonia subtilissima</i>	X		X	X		X	X	X
<i>Polysiphonia triton</i>	X			X	X	X	X	X

<i>Polysiphonia tsudana</i>	X	X					X	
<i>Polysiphonia tuberosa</i>							X	
<i>Polysiphonia</i> sp. A				X				
<i>Polysiphonia</i> sp. B			X					
<i>Polysiphonia</i> sp. C				X				
<i>Polysiphonia</i> sp. D			X	X				
<i>Polysiphonia</i> sp. E				X				
<i>Polysiphonia</i> sp. F			X					
<i>Polysiphonia</i> sp. G				X				
<i>Polysiphonia</i> sp. H				X				
<i>Polysiphonia</i> sp. I			X			X		
<i>Polysiphonia</i> sp. J								X
<i>Polysiphonia</i> sp. K	X					X		X
<i>Polysiphonia</i> sp. L	X						X	
<i>Polysiphonia</i> sp. M								X
<i>Polysiphonia</i> sp. N								X
<i>Polysiphonia</i> sp. O							X	
<i>Polysiphonia</i> sp. P								X
<i>Polysiphonia</i> sp. Q							X	X
<i>Polysiphonia</i> sp. R							X	
<i>Polysiphonia</i> -like								
Rhodomelaceae							X	
<i>Stylonema</i> sp.	X	X	X	X	X	X	X	X
<i>Taenioma perpusillum</i>	X			X	X			X
<i>Tiffaniella saccorhiza</i>		X					X	X
<i>Tolypocladia</i> <i>glomerulata</i>						X	X	X
<i>Womersleyella herpa</i>	X	X				X		
<i>Womersleyella setacea</i>	X	X			X	X		X
<i>Vertebrata foetidissima</i>			X					
<i>Vertebrata</i> sp.					X	X		X

Unidentified multiaxial Gigartinales	X							
Unidentified Rhodomelaceae								X
Laterally branching acrochaetiod	X	X	X					
Multiaxial anastomosing red							X	
Uniseriate dichotomous red	X	X				X		X

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